

# MEMOIRS

OF THE

# QUEENSLAND MUSEUM



BRISBANE  
30 JUNE 1997

VOLUME 42  
PART 1

# MEMOIRS OF THE QUEENSLAND MUSEUM

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National Library of Australia card number  
ISSN 0079-8835

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# SOME RECENT SPECIES OF THE GENUS *ANASKOPORA* WASS, 1975 (BRYOZOA: CRIBRIOMORPHA) FROM QUEENSLAND

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Arnold, P.W. & Cook, P.L. 1997 06 30: Some Recent species of the genus *Anaskopora* Wass, 1975 (Bryozoa: Cribriomorpha) from Queensland. *Memoirs of the Queensland Museum* 42(1): 1-11. Brisbane. ISSN 0079-8835.

Several species of the genus *Anaskopora* have small, globular colonies, composed principally of frontally budded autozooids, kenozooids and avicularia. Hitherto, all known species have been Tertiary fossils from Victoria. *A. parkeri* sp. nov. is a Recent species here described from the Queensland continental slope. Colonies possess long rhizoids, which are inferred to have also occurred in fossil species with the same mode of growth and colony form. *Cellepora doliaris* Maplestone, 1909, a rare conical species with more regular frontal budding, originally found from New South Wales, has been referred in the past to the genus *Reginella*. It is here redescribed from specimens collected on the continental slope of Queensland, and is reassigned to *Anaskopora*. The characters of the genus *Reginella*, which have been somewhat misunderstood, are discussed and the type species, *R. furcata* (Hincks, 1882), is redescribed. □ Bryozoa, *Anaskopora*, *Reginella*, taxonomy, morphology.

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Colonies of cribriomorph Bryozoa tend to be encrusting and unilaminar, although a few fossil species were inferred to have had a 'free-living' habit.

In this paper, we report the discovery of a new species of deep-sea free-living cribriomorph anchored by rootlets. We place the new species in the genus *Anaskopora*. Wass (1975) revised the genus *Corbulipora* MacGillivray (1895) and described several fossil species from the Victorian Tertiary, some of which he referred to a new subgenus *Anaskopora*. Recent revision of *Corbulipora* has shown that its species occur in multiple growth phases (see Bock & Cook, 1994), and that the species of *Anaskopora* are generically distinct (see Bock & Cook, in press).

The discovery of a Recent species of *Anaskopora* makes a significant contribution to the interpretation of the colony structure of fossil species, several of which can now confidently be inferred to have been anchored by rhizoid systems. Understanding of this mode of growth also allows the inference that the fossil species lived in and upon the upper layers of particulate seabottoms, and were part of a 'sand-fauna' (see Cook, 1981) of similarly adapted bryozoan species.

## METHODS

Specimens were bleached in sodium hypochlorite solution and coated with AuPd or carbon for SEM. Abbreviations used: AM, Australian Museum, Sydney; BMNH, Natural History Mu-

seum, London; MOV, Museum of Victoria, Melbourne; MTQ, Museum of Tropical Queensland, Townsville; QMG, Queensland Museum, Brisbane.

Morphological terms used in the descriptions are defined in Bassler (1953) and Boardman & Cheetham (1983).

## SYSTEMATICS

Class GYMNOAEMATA Allman, 1856  
Order CHEILOSTOMATIDA Busk, 1852  
Infraorder CRIBRIOMORPHA Harmer, 1926  
Family CRIBRILINIDAE Hincks, 1879

### *Anaskopora* Wass, 1975

*Anaskopora* Wass, 1975:170. Bock & Cook 1996; in press.

TYPE SPECIES. *Cribrilina elevata* MacGillivray, 1895.

DESCRIPTION. Colony encrusting, originating on very small substrata, often globular-to-conical. Autozooids with septulae in the vertical walls, some or all of which become surrounded by a partially calcified chamber with an upper, cuticle-covered window. Zooids budded laterally and distally, or from chambered pores (see below) as interzooidal frontal buds. Interzooidal kenozooids and avicularia, together with rhizoids in some species, produced in the same way. Au-



lozoids with a costate pericyst, with lacunae; pelmatidia rare or absent. Secondary, calcified orifice with paired spines and a raised, distal, fimbriated plate. Avicularia distal or distolateral; occasionally proximal; rostrum rounded or subtriangular, with paired condyles. Ovicells unknown.

The globular species of *Anaskopora*, in particular, possess a kind of pore chamber, here called a 'chambered pore' to distinguish it from other forms of diatellae. This originates as a calcified chamber surrounding one or more septulae in the vertical walls of zooids. The chamber is uncalcified on the frontal side, and the cuticle covering this window is able to expand intussusceptively so that the chamber may enlarge to form interzooidal kenozooids, autozooids, avicularia and rhizoids. Chambered pores occur in *Corbulipora*, but are not the regular source of frontally budded zooids, as they are in the globular species of *Anaskopora*. Some specimens of species described by Bock & Cook (in press), and a few of the colonies of *A. parkeri* (see below), originate upon very small shell substrata. These are rapidly covered by encrusting zooids with chambered pores at their corners. These pores produce an interzooidal, frontally budded series of zooids in subsequent astogenetic generations, which completely supersede any further encrusting growth. In *Anaskopora doliaris*, frontal budding of this kind seems to form the entire colony, and is very regular, so that the conical form is produced.

***Anaskopora parkeri* sp. nov.**  
(Figs 1A,B, 2A,B, 3)

**MATERIAL EXAMINED.** HOLOTYPE: QMG-21282, in alcohol, 'Cidaris I' Stn 42.2, 17°21.77'S, 146°48.52'E, 15.v.1986, 296-302m, epibenthic sledge (1/2 inch inner liner), at MTQ. PARATYPES: QMG21283, one colony mounted on SEM stub, same data as holotype; QMG21284, one colony mounted on SEM stub, same data as holotype; QMG21285, 56 colonies in alcohol, same data as holotype; MQVF80820, 9 colonies in alcohol, same data as holotype. **ADDITIONAL MATERIAL:** QMG21288, 71 colonies in alcohol, same data as holotype; QMG21289, 2 colonies in alcohol, 'Cidaris I' Stn 43.2, 17°34.58'S, 146°53.21'E, 15.v.1986, 458-500m, epibenthic sledge (1/2 inch liner), at MTQ.

**ETYMOLOGY.** For the late Shane Parker, of the South Australian Museum.

**DESCRIPTION.** Colonies 0.50-5.0mm in diameter, encrusting small foraminiferans or completely free-living (Fig. 1A), anchored by large rhizoids (Fig. 1B). Autozooids with frontal shield

of 18-24 costae alternating with rows of 7-8 lacunae (Fig. 2A). Calcified orifice with one pair of flattened, sometimes terminally bifid, lateral-oral spines (Fig. 2A), paired lateral condyles and a raised distal plate with 5-8 fimbriations (Fig. 2B) and a pit at the base of the outer surface (Fig. 3). Operculum golden-brown, with a marginal sclerite, filling the secondary orifice. Septulae 2-3 distal, 3-4 lateral, becoming surrounded by chambered pores (Fig. 3) which develop frontally as a series of 4-6 small kenozooids with cuticular frontals, surrounding each zooid. Avicularia distolateral (Figs 2A, 3), developed from chambered pores; occasionally paired or even proximal. Subrostral chambers raised, rounded (Fig. 3); mandibles with a marginal sclerite, oriented laterally. Zooids budded in alternating interzooidal series from chambered pores, oriented irregularly, colony forming an ectoproctolith (Figs 1A, 2A, 3). Interzooidal kenozooids becoming extrazooidal.

Colony and zooid dimensions are given in Table 1.

**REMARKS.** *A. parkeri* closely resembles *A. cornuta* (MacGillivray, 1895), which was referred to *Corbulipora* by Wass (1975) but reassigned to *Anaskopora* by Bock & Cook (in press). The two species have similar colony structures, and the autozooids of *A. cornuta* have numerous straight rows of costae, alternating with small lacunae, like those of *A. parkeri*. *A. cornuta* differs in the distal position of the avicularium, which is not nearly as prominent as that of *A. parkeri*. The two species are so alike that it seems certain that the Victorian Tertiary species was a direct ancestor of the Recent form from Queensland. It may also be inferred with a high degree of confidence that the colonies of *A. cornuta* possessed rhizoids and lived in a similar micro-environment to that inhabited by *A. parkeri*.

Of 75 colonies of *A. parkeri* from Stn 42.2, 20 had well developed rhizoids which were 2-3mm long and, when turgid, 0.33-0.38mm wide. The colonies exhibited a developmental series; the smallest had 6 zooids, the largest approximately 50 autozooids visible at the surface. Where the youngest stages encrusted small foraminifera there was a large, cuticle-covered cavity next to the primary zooid; in two cases, with a large rhizoid beside it. Whether the cuticle-covered cavity is the ancestrula is not known. The rhizoids themselves terminated in numerous rootlets which had shell fragments and foraminiferans adhering to the cuticle. One colony was the substratum for a small colony of a tubuliporid cyclo-

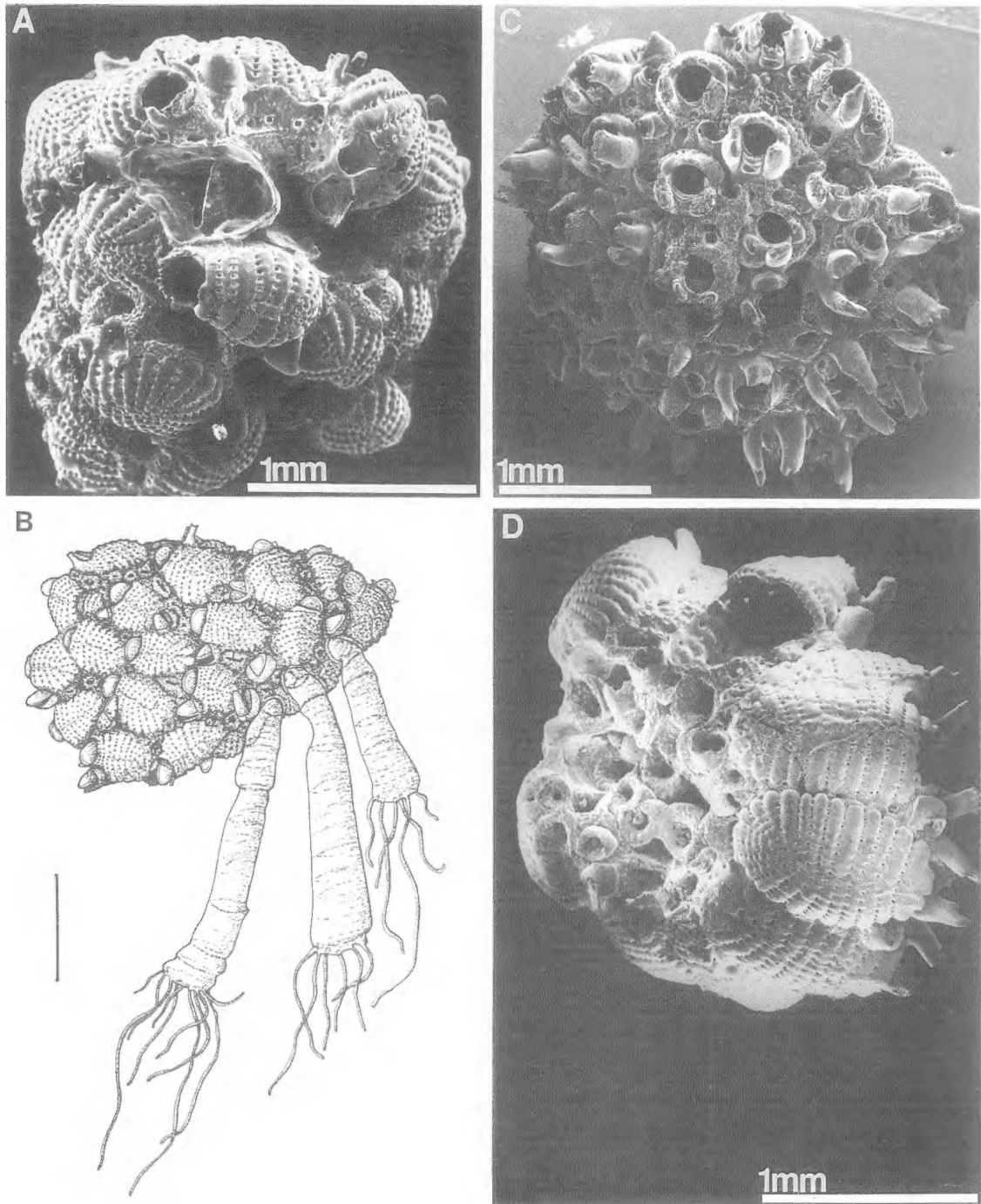


FIG. 1. A-B, *Anaskopora parkeri* sp. nov. A, QMG21283, frontally budded colony, x 32; B, Sketch of colony with rhizoids, x 15. C-D, *A. doliaris* (Maplestone). C, QMG21286, colony from frontal side, x 21; D, QMG21287, colony from basal side, x 31.

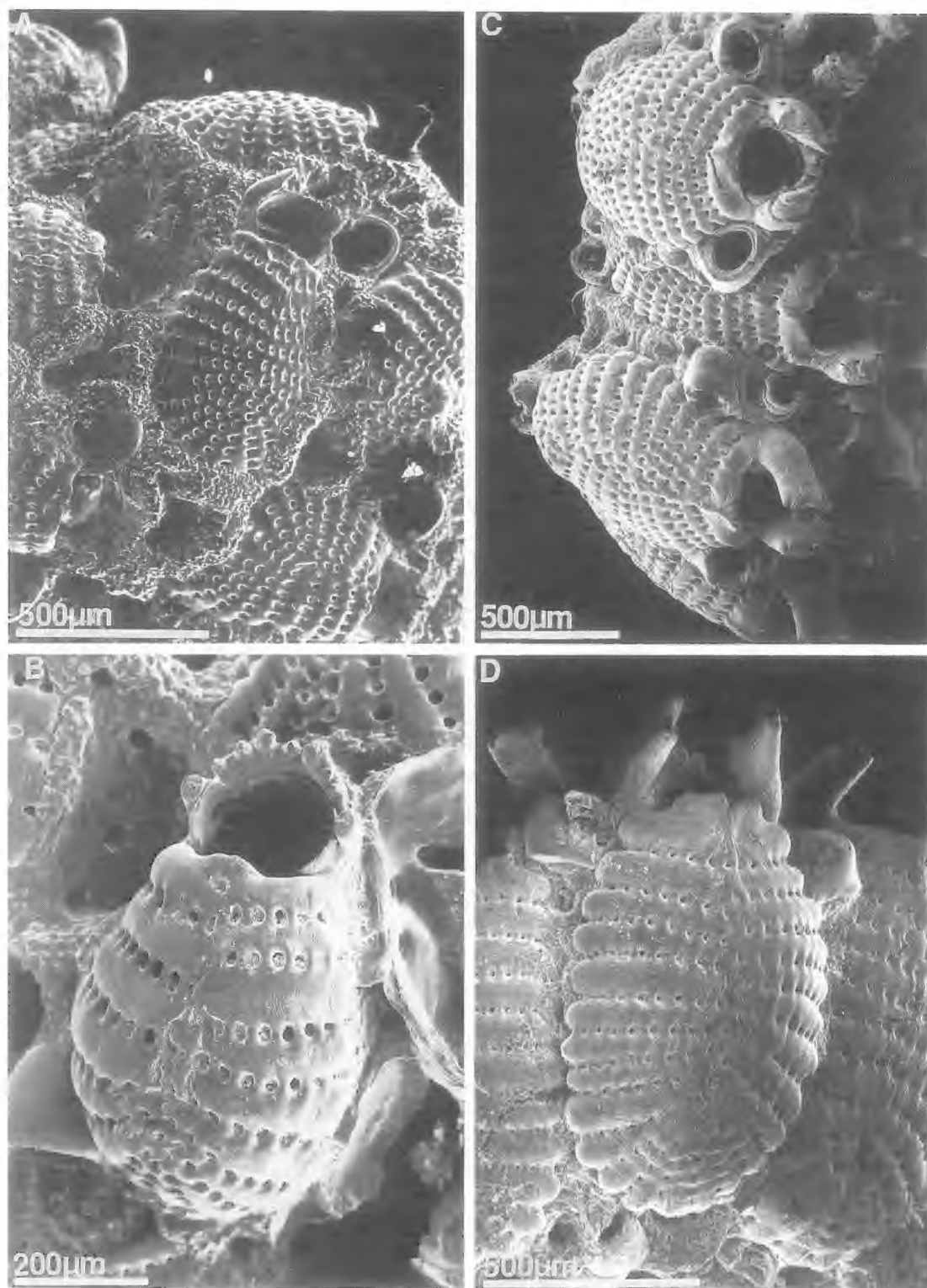


FIG. 2. A-B, *Anaskopora parkeri* sp. nov. A, QMG21284, general view of zooids, x 58; B, QMG21283, enlarged view of one zooid, x 100. C-D, *A. doliaris* (Maplestone). C, QMG21286, general view of zooids, x 42; D, QMG21287, enlarged view of one zooid, x 66.

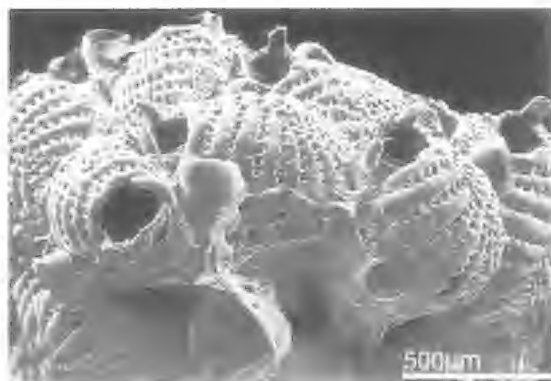


FIG. 3. *Anaskopora parkeri* sp. nov., QMG21283. Autozooids showing details of orifices and frontal buds,  $\times 37$ .

stome. Two others had the horny skeleton of *Stephanoscyphus* (Scyphozoa: Coronatae) growing on them; Lagaij (1963) described a similar case in which a hydroid grew on the globular colonies of *Fedora nodosa*.

The specimens of *A. parkeri* were accompanied by other rooted species associated with sand-faunas. These included *Parmularia* sp., *Parastichopora vanna* (see Cook & Chimonides, 1981) and *Conescharrellina* sp.

***Anaskopora doliaris* (Maplestone)**  
(Figs 1C,D, 2C,D, 4A,B)

*Cellepora doliaris* Maplestone, 1909: 272, Pl. 77, Figs 10 A,B.

*Reginella doliaris* Brown 1958: 53; Hastings 1964: 254, Pl. 1, Figs 1-3, Pls 2 and 3.

LECTOTYPE (indicated here): AMU201, 22 miles (35.4 km) East of Port Jackson, New South Wales, 80 fath. (146 m), HMCS 'Miner', labelled 'TYPE'. PARALECTOTYPE: BMNH1909.11.12.14, as above.

MATERIAL EXAMINED. QMG21286, G21287, 'Cidaris 1' Stn 43.2, 17°34.58'S, 146°53.21'E, 15.v.1986, 458-500 m, epibenthic sledge (1/2 inch inner liner), 2 colonies on SEM stubs; at MTQ.

DESCRIPTION. Colony conical, one autozooid thick (Fig. 1D), inferred to be anchored by basal rhizoids. Autozooids erect, deeply immersed and oriented with the distal part of the orifice towards the ancestrula and the centre of the colony (Fig. 1C). Each autozooid with a series of simple septulae in the lateral, distal and proximal walls (Fig. 4B), all septulae becoming included in a series of chambered pores which develop frontally into new autozooids or avicularia (Fig. 4B).

The budding of autozooids is regular and radial, each astogenetic generation of autozooids alternating with one of kenozooids (Fig. 2C). Autozooid frontal shield with about 25 closely spaced costae, the distal costae thickened as an apertural bar which may be weakly bifid or thickened to form a median ridge (Figs 2C,D). Costae alternate with regular rows of 7-8 fine lacunae on each side of the mid-line. Secondary calcified orifice rounded, with a pair of flattened, curved bifid to trifid oral spines (Fig. 2D), a raised, fimbriated distal plate with 3 denticles (Fig. 4A) and distal pit (Fig. 4A), and a pair of condyles. Avicularia usually paired, oral (Fig. 2C), or single, proximal (Figs 1D, 4B); rostra raised, with paired condyles (Fig. 2C). Basal surface of cone hollow, with large paired foramina surrounded by kenozooids and avicularia budded round the proximal ends of the successive generations of erect autozooids (Fig. 1D).

Colony and zooid dimensions are given in Table 1.

REMARKS. Maplestone (1909) described the colony as encrusting, but there was no sign of any substratum in specimens we examined. Of the 39 species listed by Maplestone (1909) associated with *A. doliaris* from New South Wales, 11 were new to science and 15 had a sand-fauna (see Cook, 1981) adapted colony form. Of these, 10 had rhizoids (7 species of *Conescharrellina*, 1 of *Zeugladora*, 1 of *Sphaeropora*, and 1 of *Anaskopora*), and 5 were free-living, lunulitiform species (1 of *Lunularia*, 3 of *Selenaria* and 1 of *Orionella* spp.).

Hastings (1964) gave a very full description and interpretation of colony growth and relationships in *C. doliaris*. She noted the development of kenozooids from septulae, and figured and described the distal fimbriated plate. However, her account was written before the explanation of frontal budding by Banta (1972) and of reversed frontal budding by Cook & Lagaij (1976). Hastings used the structure of the ascophoran genus *Conescharrellina* in her comparisons. The budding pattern is analogous in the two examples, although the type of frontal bud produced is quite different in *Conescharrellina*. Hastings (1964: 258; 1966: 68) noted the similarities in development of intercalated avicularia and kenozooids in *C. doliaris* and *Membraniporella agassizii* Smitt (1873: 11, Pl. 5, Figs 103-106), from Florida. *M. agassizii* is erect and quadriserial; the autozooids have costae without either pematidia or lateral costal fusions (see also Ristedt, 1979, Pl. 2, Figs



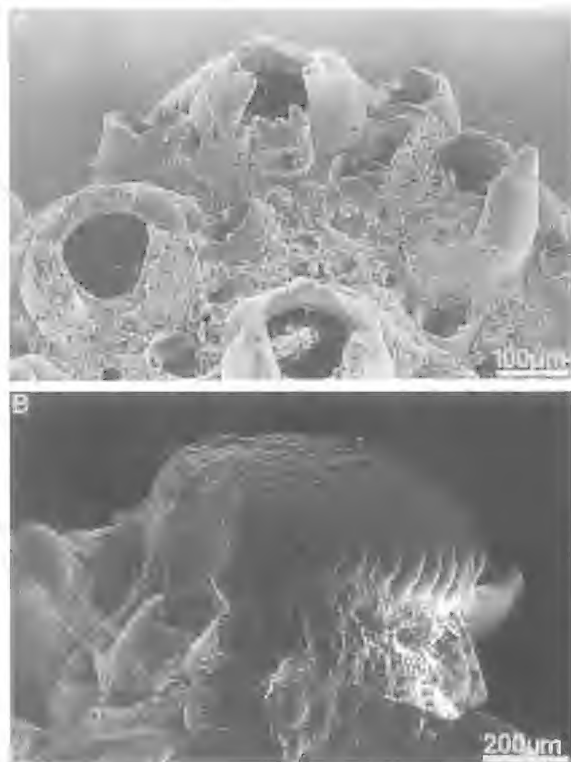


FIG. 4. *Anaskopora doliaris* (Maplestone). A, QMG21286, details of orifices, x 90; B, QMG21287, details of kenozooids, x 55.

1, 2). The gymnocyst is distinct early in ontogeny, but later changes produce avicularia and kenozooids surrounding the autozooids which eventually obscure all but the orifices on the frontal surface of branches. The origin of the kenozooids and avicularia has not been described, but may be inferred to be from chambered pores similar to those in *Anaskopora*. They appear to strengthen the delicate, erect branches. Hastings (1964) also emphasized the similarities in interzooidal budding from the pore-chambers of *Hippothoa* with the budding of kenozooids in *C. doliaris*. The similarities in pore-chamber and chambered-pore structure are discussed by Bock and Cook (in press).

*Anaskopora doliaris* is known from only 4 colonies. The lectotype and paralectotype were both from the 'Miner' collections, one specimen having been sent by Maplestone to the then British Museum (Natural History) as a 'cotype'. We infer that the two colonies of *Anaskopora doliaris* from the 'Cidarid 1' collection were anchored by rhizoids like those of *A. parkeri*, which probably emanate from the large, paired foramina on the

basal surface (Fig. 2C). It differs from *A. parkeri* and the other globular, fossil species, *A. elevata*, *A. cornuta* and *A. rotundata* (see Bock & Cook, in press), in the regularity of its reversed frontal budding and hollow basal surface. It resembles other species of *Anaskopora* in the mode of development and distribution of interzooidal kenozooids and avicularia, and the presence of distal fimbriated plate in the autozooids. The reasons for its removal from the genus *Reginella* are related to the history of the concepts and the characters of that genus which are discussed below.

### *Reginella* Jullien, 1886

The attribution of *Cellepora doliaris* Maplestone, 1909 to the genus *Reginella* by Hastings (1964) seems to have been the result of a series of misconceptions which have had several repercussions in the later interpretation of Australasian and other cribrimorph species.

*Reginella* was introduced by Jullien (1886: 605) as a genus of Costulidae (=Cribrulinidae), for *C. furcata* Hincks (1882: 470, Pl. 20, Fig. 5), a Recent species from the coast of British Columbia. No other species was included. Jullien's definition was not based upon the examination of specimens, but was an interpretation of Hincks's description and figure. Canu & Bassler (1929: 243) provided a literal English translation of Jullien's generic description, which mentioned that the frontal shield was composed of 'voluminous ribs much in relief', and that the 'intercostal furrows traverse entirely the zooecium and separate completely each pair of transverse ribs'. Pelmaticia were described as decreasing in size from the margin along each costa, and the lacunae were noted as each occupying 'the middle of a calcareous polygonal cell'. Osburn (1950: 179, Pl. 28, Fig. 3) redescribed *R. furcata* from Californian specimens, and noted that septulae were present, that the brooding zooid orifices were dimorphic, that the large ovicells were punctate and had a median keel, and that the oral spines were often absent. Hastings (1964: 253) also redescribed *R. furcata* from Hincks's British Columbian material and noted that Jullien's 'polygonal cells' were 'no more than an effect of light and shade'. There are, however, other discrepancies between Hincks's (1882) description and Jullien's (1886) definition. Hincks emphasized that the costae were only 'slightly raised', and that the intercostal 'grooves' were 'shallow' and were arranged 'radiating to the median line'.



TABLE 1. Comparative measurements of colony, autozoid and avicularium in *Anaskopora parkeri* and *A. doliaris*. Original measurements calculated from scanning electron micrographs. Width of lacuna in microns; all other measurements in millimetres. The frontal shield length marked by an asterisk is a probable misprint in Hastings (1964). Autozoid length is considered the same as frontal shield width.

	<i>A. doliaris</i> (Hastings 1964)	<i>A. doliaris</i> (original)	<i>A. parkeri</i> (original)
Colony dimensions	~ 3.5 x 3	2.9 x 3.3	0.5 - 5
Autozoid length	-	1.06, 1.06, 1.08	0.69, 0.72, 0.76, 0.68
Frontal shield length, width	0.1* x 0.5	0.95, 1.01 L, 0.66, 0.70 W	0.49, 0.60 L, 0.41 W
Aperture autozoid	-	0.21, 0.22, 0.22 L, 0.22, 0.24, 0.24 W	0.14, 0.15 L, 0.17, 0.18, 0.21 W
Apertural bar width	-	0.15	0.05, 0.07
Lateral oral spine	-	0.3, 0.4, 0.4, 0.4 L, 0.2, 0.2 W	0.1, 0.1 L, 0.06, 0.06 W
Number of denticles on fimbriated plate	2	2-3	5-8
Width of pit at base of fimbriated plate	-	0.07, 0.07, 0.10	0.06
Number of costae	9-13 (one side only)	10-25	18-24
Width of costae	-	0.07, 0.07, 0.09, 0.09	0.03, 0.03, 0.03, 0.04, 0.06, 0.06, 0.06, 0.09
Number of lacunae per side	-	5-8	7-8
Width of lacunae	-	9-10	10-25
Height of oral avicularium	-	0.18, 0.19	0.14
Aperture of oral avicularium	-	0.16, 0.16 L, 0.12, 0.10 W	0.17, 0.17, 0.17 L, 0.13, 0.13, 0.13 W
Width of basal kenozooidal chambers	-	0.16, 0.19, 0.29	not applicable

This is in contrast to Jullien's prominent costae, and furrows which traversed the zooid horizontally. Cook (1985: 123) also examined Hincks's specimens of *R. furcata* and noted that the costae were broad and flattened, with pematidia and small lacunae, and remarked 'the relationship of *R. furcata* with the various species subsequently assigned to *Reginella* requires investigation'. The type and other specimens of *R. furcata* have been re-examined, and a short description is given below.

#### *Reginella furcata* (Hincks)

*Cribrilina furcata* Hincks, 1882: 470, Pl. 20, Fig. 5.  
*Reginella furcata* O'Donoghue & O'Donoghue 1926: 52; Osburn 1950: 179, Pl. 28, Fig. 3; Hastings 1964: 253; Soule et al. 1995: 123, Fig. 42 A-C.

**MATERIAL EXAMINED.** BMNH1886.3.16.18, Queen Charlotte Islands, Hincks Coll. on 4 shell fragments; 1921.11.17.12 and 1968.1.18.100, Departure Bay, Vancouver Island, O'Donoghue Coll.; 1986.9.10.3 Cannon Beach, Western Washington, L. Pitt Coll.

**DESCRIPTION.** Autozooids encrusting, colony originating from a membraniporiform ancestrula with long marginal spines. Zooidal gymnocyst very narrow, vertical walls shallow. Frontal

shield of 11-17 flattened costae, each with 3-4 pematidia. Suboral bar variously thickened, sometimes with a minute central mucro. Costae irregularly fused with a shallow central suture; the distal pairs of costae extending horizontally, the proximal 5-7 pairs converging distally and medially. Intercoastal furrows narrow, with 4-6 rounded lacunae. Six evanescent oral spines, one lateral pair often remaining, and becoming thickened, or extended frontally and bifurcated terminally. Zooids communicating through 2 distal and 3 lateral groups of septulae, each enclosed in a very shallow, slit-like chamber at the base of the gymnocyst. Ovicells large, hyperstomial, with a median suture line and 16-20 small, rounded or irregular pores scattered over the surface; fertile orifices very slightly wider than autozoid orifices. Avicularia absent.

**REMARKS.** Osburn (1950) illustrated a single zooid of his Californian material of *R. furcata*. The drawing is misleading, as it resembles Jullien's concept of *Reginella* rather more than Hincks's description of *R. furcata*. The zooid appears to be at a late ontogenetic stage, with thickened, but not prominent, costae and the lines of lacunae traverse the frontal shield horizontally, with no obvious median suture line. Pematidia were reported to be present but were not

illustrated. Osburn (1950: 180, Pl. 28, Fig. 4 and Pl. 29, Fig. 3) also illustrated another Californian species as *Reginella mucronata*, which had originally been introduced for Pleistocene material from the same region by Canu & Bassler (1923: 92, Pl. 35, Fig. 4). Canu & Bassler (1923) referred it to the genus *Metracolpota* Canu & Bassler (1917). Canu & Bassler's (1923) retouched photographs show zooids very similar to that illustrated by Osburn for *R. furcata*, rather than the rounded zooids with large lacunae he illustrated for *R. mucronata*. Hastings (1964: 253) considered that these two species were identical, although Soule (1959: 46), who had examined both fossil and Recent material, had regarded *R. mucronata* as distinct. The genus *Metracolpota* was originally introduced for the Eocene species *M. robusta* Canu & Bassler (1917: 35, Pl. 3, Fig. 6; and 1920: 308, Pl. 43, Figs 1-7), from North Carolina. *M. robusta* and the other Eocene species described by Canu & Bassler were all illustrated by heavily retouched photographs, many of elongated zooids with uninterrupted lines of lacunae extending across the frontal shield, with little or no indication of a median suture line. *M. robusta* has large, erect, bilaminar colonies and zooids with paired oral avicularia. The ovicells are very large and ridged centrally, but not punctate like those of *R. furcata*. Generally, *M. robusta*, the type species, and the other Eocene forms assigned to *Metracolpota*, have little in common with, and are distinct from, *Reginella*. We accept that the Pleistocene-to-Recent *M. mucronata* is congeneric with *R. furcata*, but this provides no justification for regarding the genus *Metracolpota* as a synonym of *Reginella*. That idea had been very tentatively suggested by Osburn (1950) but was later greatly extended by Hastings (1964) in order to include other species with avicularia within the generic description (see below).

Jullien's (1886) definition and the studies just cited so modified the generic concept of *Reginella* that it now included characters quite unlike those of its type species. This would explain the implicit referral of *Cribrilina vas* Brown, 1954, a Pliocene species from New Zealand, to *Reginella* by Brown (1958), when discussing a somewhat similar species from the Tertiary of Victoria, *Reginella maplestonei* Brown, 1958. Neither species has avicularia, but small, peristomial ovicells were illustrated in *R. maplestonei*. Powell (1967: 221, Pl. 2, Fig. 6, Fig. 4) redescribed *R. vas* from Recent New Zealand specimens, noting its elongated zooids, absence

of pematidia, and small, imperforate, peristomial ovicells; all characters completely unlike those of *R. furcata*. Brown (1958) also included the Recent, Antarctic *Cribrilina projecta* Waters, 1904, which has small oral avicularia and distinct pematidia, in his concept of *Reginella*. Hastings (1964) considered that *C. projecta* was not congeneric with *R. furcata*, but gave no evidence for her conclusion. Moyano (1985) introduced the genus *Dendroperistoma* for *C. projecta*.

The characters of *Cellepora doliaris* Maplestone, 1909 also became involved in the *Reginella* problem, when Brown (1958:53) mentioned that Hastings (presumably in litt.), 'has also pointed out a very close resemblance in the nature of the frontal shield between *C. vas* and *Cellepora doliaris* Maplestone'. Hastings, however, did not redescribe *C. doliaris* for a further 6 years. When she did, she remarked (1964: 258, footnote 1), with a reference to Brown (1958), that Brown had told her in 1955 that he had 'referred *Cribrilina alcicornis* and *Cellepora doliaris* to *Reginella*' when, in fact, Brown (1958) had never mentioned *C. alcicornis* at all (see below).

*C. alcicornis* Jullien (1883: 508, Pl. 14, Figs 23-25) is a deep-water, encrusting species from the Northeastern Atlantic. Autozooids have costae with no pematidia, and four, large, branched oral spines. Interzooidal avicularia and large interzooidal kenozooids are budded among the autozooids, and the elongated ovicells are not punctate. *C. alcicornis* is therefore unlike *R. furcata*, and it is significant that Jullien (1886) did not include *C. alcicornis* when introducing *Reginella*, and that later, Calvet (1907:399) and Prenant & Bobin (1966: 578, Fig. 200), continued to refer the species to *Cribrilina*. More recently, both d'Hondt (1974: 47, Fig. 7) and Harmelin (1978: 178, Pl. 1, Fig. 3, Figs 3-4), who examined additional Atlantic material, also maintained *C. alcicornis* in *Cribrilina*. Harmelin noted that one of Hastings's 'points of resemblance' between *C. doliaris* and *C. alcicornis* was based on the mistaken assumption that Jullien's (1886) phrase 'grande ponctuations' referred to the interzooidal kenozooids, whereas in fact, it referred to the intercostal lacunae. He remarked 'Le changement de genera ne semble pas justifié pour cette espèce'.

Quite apart from this confusion, it is unfortunate that Hastings (1964: 252) extended Osburn's (1950) tentative synonymy of *Metracolpota* with *Reginella*, including some of the characters of the Eocene *M. robusta*, such as avicularia, in her

concept of *Reginella*. Thus the presence of numerous avicularia in *C. doliaris*, which are totally absent in *R. furcata*, did not preclude its referral to *Reginella*, because avicularia had become a 'generic character'. In the same way, the presence of kenozooids with the avicularia in *C. doliaris*, was mitigated by the tacit assignment of *Cribrilina alcicornis*, which has both, to *Reginella*, although neither were present in *R. furcata*. The presence of avicularia and kenozooids in both *C. alcicornis* and *C. doliaris* is interesting, but the structures differ completely in their origins and general morphology between the two species. In any case, neither has anything to do with the characters of the genus *Reginella*. Two North American species which have been referred to *Reginella* also require further investigation. *Reginella floridana* (Smitt, 1873) has been described by Winston (1982) from Florida, and by Cook (1985) from West Africa. No ovicells have ever been found in any specimen of this species. *R. repangulata* Winston & Håkansson, 1986, from an interstitial Floridan fauna, has ovicells somewhat similar to those of *R. furcata*.

It is obvious that by this time the original characteristics of the genus have become completely submerged by the accumulation of additional or alternative features derived from the diversity of species included. This is illustrated by Gordon (1984: 63, Pl. 20, Figs D-E), who redescribed *Reginella* *var.*, and introduced a new, uniserial encrusting species from New Zealand, *R. stolonifera* Gordon (1984: 63, Pl. 20, Figs A-C), which had large, branched oral spines like those of *C. alcicornis*. The concept of the genus was now extended to include all the disparate forms mentioned above, from the Arctic, Antarctic, Atlantic and Pacific Oceans, from deep and shallow, even interstitial waters, and from the Tertiaries of North America, Australia and New Zealand. The generic characters now encompassed: colonies encrusting, erect and bilaminar, and conical; zooids uniserial to contiguous and frontally budded, avicularia present or absent; ovicells hyperstomial and peristomial with or without pores or fenestrae; pore chambers present or absent. To these may be added, peltatidia and kenozooids present or absent. The only consistent characters are 'slit-like intercostal lacunae', and 'costae arranged in straight rows across the zooid, often traversing the mid-line without interruption'. Although these features occur late in ontogeny in *R. var.* and *R. stolonifera*, neither occurs in *R. furcata*.

In conclusion, it is obvious that *Reginella* should be restricted to Recent and Pleistocene species from the North American and Japanese Pacific coasts, and that *Metracolpoda* should be retained only for the American Eocene species. Soule, Soule & Chaney (1995) give notes on *Reginella furcata* and introduce a new genus, *Reginelloides*, for *R. stolonifera* Gordon, 1984. *Cribrilina alcicornis*, *C. var.* *Reginella maplestoni*, *R. floridana* and *R. repangulata* should also be re-investigated, and new generic groups should be introduced for their reception where necessary.

The colonies of *R. furcata* from Vancouver Island examined by one of us (PLC) included about 20 with ancestrulae present. The ancestrulae had small pore-chambers distally and laterally, and 12 long spines surrounded the opesia. Mawatari (1988: 149, Figs 9-14) has described specimens from Hokkaido, Japan, as *Reginella furcata*, and discussed previous Japanese records in detail. These include the species described as *Lyrula multipora* by Sakakura (1935: 109, Pl. 8, Fig. 7), and as *Figularia multipora* by Silén (1941: 117, Figs 178-180). All these Japanese records differ from *R. furcata* very slightly, in the complete lack of oral spines, even in early ontogeny, the raised mucros beside the orifice which give it a subtriangular appearance, and the lack of any dimorphism in the fertile orifices. Osburn (1950) described several nominal taxa from the Arctic to the Mexican coasts of North America and referred them to *Reginella*. They all resemble *R. furcata* in possessing straight, converging rows of lacunae, paired oral spines and large ovicells with a central suture and punctate surface. Until the actual limits of variation of these species, especially those from California, like *R. mucronata*, have been analysed, it is probably best to maintain them, together with *R. multipora*, as distinct species of *Reginella*.

#### ACKNOWLEDGEMENTS

We thank Dr P.E. Boek (Royal Melbourne Institute of Technology) for his help and interest. Ms M. Spencer Jones (Natural History Museum, London), for the loan of specimens of *Reginella furcata* and Dr P. Berents (Australian Museum) for confirming details of Mapleston's type of *C. doliaris*. The 'Cidarid' expeditions on R.V. 'Franklin' were partially funded by an Australian Marine Science and Technology Grant to Prof. M. Pichon.

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**SYNONYMY OF *CTENOTUS MONTICOLA* STORR, 1981 AND *CTENOTUS HYPATIA* INGRAM AND CZECHURA, 1990.** *Memoirs of the Queensland Museum* 42(1): 12, 1997. - *Ctenotus monticola* and *C. hypatia* are medium-sized. Both are classed 'poorly known' (McDonald et al., 1991). The former has a 'a very restricted distribution with a maximum geographic distribution of less than 100 km'. The latter is '... known only from the type collection'. *C. monticola* was described from a series of specimens collected '11 km W of Mareeba, Queensland (17°02'S, 145°20'E)'. The type locality of *C. hypatia* is 'granite gorge, 15 km W of Mareeba, (17°00'S, 145°17'E)'. These localities are both on Granite Ck, approximately 6 km apart (J. Covacevich pers. comm.). That, and the fact that the type descriptions of *C. monticola* and *C. hypatia* are very similar, prompted a re-examination of the type material of each to determine whether or not they are distinct.

Re-examination of the type specimens and type descriptions indicates that *C. monticola* and *C. hypatia* are conspecific (Table 1). Almost without exception, the measurements and scale characters of *C. hypatia* fall well within the range of values provided by Storr (1981) for *C. monticola*. The differences in elongation, indicated by the chin-vent and paravertebral counts are inconsequential. Greater variation is frequently recorded in a single species (e.g. *C. astictus* Horner, 1995 & *C. stuarti* Horner 1995). Additionally, both type specimens share the following characters: nasals separated; nasal groove absent, rostral and frontonasal in narrow to moderate contact; second loreal 1.2 times as wide as high; prefrontals large and separated, frontal long and narrow contacting the prefrontals, the frontonasal, the first 3 supraoculars, and the frontoparietals, 4 supraoculars, 2nd the largest; 1st supraciliary the largest, 4th to penultimate considerably smaller than others; 5th supralabial subocular; ear aperture large; toes compressed.

Colour and pattern are known to be useful in distinguishing some species of *Ctenotus* (e.g., *C. arcatus* Czechura & Wombey, 1982 and *C. robustus* Storr, 1970). However, this is not the case with *C. monticola* and *C. hypatia*. Colour and pattern of the type specimens of *C. monticola* (5) and *C. hypatia* (1) have been detailed by Storr (1981) and Ingram & Czechura (1990). Variation in the former fully covers the latter.

Thus, in every respect (meristics, scalation, colour/pattern) there are no significant differences between *C. monticola* and *C. hypatia*. *Ctenotus monticola* Storr, 1981 is, therefore, a senior synonym of *C. hypatia* Ingram & Czechura, 1990.

#### Acknowledgements

We thank Jeanette Covacevich for reading and suggesting improvements to this note.

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TABLE 1. Comparison of holotypes of *C. monticola* (QMJ39468) and *C. hypatia* (QMJ42092). Values in parentheses are from the type descriptions.

Character	Species	
	<i>C. monticola</i> (QMJ39468)	<i>C. hypatia</i> (QMJ42092)
Snout-vent (mm)	53 (51-61)	55 (54)
Foreleg (%SVL)	25 (22-25)	25 (NA)
Hindleg (%SVL)	44 (39-45)	44 (44)
Tail (%SVL)	NA (211-220)	215 (215)
Head width (%SVL)	13 (NA)	12 (12)
Head length (%SVL)	20 (NA)	19 (NA)
Supraciliaries	8 (7 or 8)	8 (9)
Upper ciliaries	9/11 (9-11)	8/9 (NA)
Presuboculars	2 (2, rarely 3)	2 (NA)
Upper labials	7 (7)	7 (7)
Ear lobules	2 or 3 (3-5)	3 or 4 (3-4)
Largest ear lobule	1 (1 usually largest)	1 or 2 (NA)
Enlarged pairs of nuchal scales	4-5 (3-5)	4-5 (4-5)
Midbody scale rows	26 (24-28)	28 (28)
No. of scales from chin-vent	76 (NA)	82 (75)
Paravertebral scale rows	67 (NA)	72 (NA)
Subdigital lamellae	18/19 (17-19)	18/19 (20)
Structure of subdigital lamellae	moderately wide callus (narrow to moderately wide callus)	narrow callus (keeled)

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A NEW GENUS OF HIPPOLYTID SHRIMP (CRUSTACEA: DECAPODA:  
HIPPOLYTIDAE) FOR *THOR MALDIVENSIS* BORRADAILE

A.J. BRUCE

Bruce, A.J. 1997 06 30: A new genus of hippolytid shrimp for *Thor maldivensis* Borradaile. *Memoirs of the Queensland Museum*, 42(1) 13-23. Brisbane. ISSN 0079-8835.

A new genus *Thorina*, is designated to accommodate the hippolytid shrimp *Thor maldivensis* Borradaile 1915. The new genus is distinguished from *Thor* particularly by the short, unidentate rostrum and the absence of an appendix masculina from the male second pereiopod, with marked sexual dimorphism of the first pereiopods. First recorded from the Maldiv Islands, the species is sparsely recorded throughout the Indo-West Pacific region and newly recorded from Tanganyika, Mauritius, Seychelle Islands, Western Australia, the Great Barrier Reef, Papua New Guinea, Tonga, Cook and Society Islands. □ *Natantia*, *Hippolytidae*, *Thorina*, *Indian Ocean*, *Pacific Ocean*.

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In his study of the hippolytid shrimps of the *Albatross Expedition*, Chace (in press) indicated the anomalous systematic position of *Thor maldivensis* Borradaile 1915. He clearly defined the characters of the genus *Thor* Kingsley s. str., and lists five major characters that distinguish *T. maldivensis* from all other species of the genus *Thor*, omitting it from his key to the species of that genus. A new monospecific genus for the reception of this species is here formally established. The original description of *Thor maldivensis* provided by Borradaile (1915) consisted of a brief diagnosis only but a short more detailed account with an illustration of a ♂ example was published in Borradaile (1917). This account remains the most detailed available of this species, which has been only infrequently recorded in the zoological literature.

Abbreviations used: CL, postorbital carapace length; MNHN, Museum national d'Histoire Naturelle, Paris; NTM, Museums and Art Galleries of the Northern Territory, Darwin; QM, Queensland Museum, Brisbane.

SYSTEMATICS

Class CRUSTACEA  
Order DECAPODA  
Suborder NATANTIA  
Infraorder CARIDEA  
Family HIPPOLYTIDAE

*Thorina* gen. nov.

**DIAGNOSIS.** Small hippolytid shrimps of sub-cylindrical body form. Rostrum very short, slender, acute, not exceeding proximal segment of

antennular peduncle, with single small dorsal tooth only. Carapace without carinae; supraorbital, non-articulate antennal spines present, hepatic and pterygostomial spines absent. Antennular peduncle with proximal segment with moveable plate distally, upper flagellum brush-like. Scaphocerite mid-laterally unarmed. Eyes well-developed, cornea hemispherical. With elongate acute median process anterior to first thoracic sternite. Mandible without palp, with incisor process, maxillipeds with epipods and well developed flagella on exopods. Pereiopods without arthrobranchs, epipods on exopods. First pereiopod with fingers greater than 1/3 of palm length; fingers without interlocking terminal spines, merus with ventral teeth, chelae usually greatly hypertrophied in some ♂♂. Second pereiopod with carpus with 6 segments. Propods of last 3 pereiopods not multiarticulate. Abdomen non-carinate, without dorsal teeth, with anterior 3 pleura rounded, posterior 2 posteroventrally acute, 6th abdominal segment without articulated posteroventral plate. ♂ second pleopod without appendix masculina and appendix interna. Telson with 3 pairs of dorsal spines, 3 pairs of posterior spines.

**TYPE SPECIES.** *Thor maldivensis* Borradaile, 1915.

**ETYMOLOGY.** From *Thor*, a hippolytid generic name first used by Kingsley, 1878, and -ina (Latin), diminutive. Gender, feminine.

**SYSTEMATIC POSITION.** Closely related to *Thor* Kingsley, with which most generic characters are shared and emphasised by the presence of a triangular mobile plate on the distal segment of the antennular peduncle, a feature otherwise

found to occur only in *Thor*. Distinguished from *Thor* by the greatly reduced rostrum with only a single dorsal tooth, marked sexual dimorphism of first pereopods, reduced sexual dimorphism of 3rd pereopods, presence of 3 pairs of posterior telson spines instead of 1-2 pairs, and particularly, the complete absence of an appendix masculina and appendix interna on the  $\delta$  2nd pleopod. The strongly distolaterally spinose meri of the hypertrophied  $\delta$  1st pereopods are also characteristic, but it may be noted that a single small articulated spine may be present in the West Atlantic species *Thor dobkinsi* Chace (1972). In *Thorina*, the spines are non-articulate denticular processes.

***Thorina maldivensis* comb. nov.**  
(Figs 1-6)

*Thor maldivensis*. Borradaile, 1915: 208-209; 1917: 401-402, pl. 56 fig. 6; Kemp, 1916: 391; Edmondson, 1925: 6; 1946: 252, 253, fig. 153d; Holthuis, 1953: 53-54; Bruce, 1976: 51; Kamezaki, et al., 1988: 81, col. pl.; Chace, in press.

**MATERIAL EXAMINED.** QMW19914, 1  $\delta$ , 1 ovig. ♀, stn DF/37, Heron Island, Capricorn Islands, Queensland, 3.0m, 16 October 1976, coll. D.F. Fisk. QMW21438, 1  $\delta$ , 1 ovig. ♀, stn AJB/162, Jadini, Kenya, 22 December 1972, c. 0.4m, lagoon, in *Acropora*, coll. A.J. Bruce. QMW21439, 1  $\delta$ , Aldabra, Seychelle Islands, 3 November 1964, from coral in channel reef, intertidal, coll. A.J. Bruce. QMW21440, 2 spms, macerated, Ras Iwatine, Mombasa, Kenya, 8 February 1972, lagoon, in *Millepora*, coll. A.J. Bruce. QMW21441, 1  $\delta$ , 1 ovig. ♀, stn 140, Kirwetu, Kenya, 3°46.7'S 39°50.9'E, low water spring tide level, 6 November 1971, coll. A.J. Bruce, reef flat, under dead coral. QMW21442, 4 ovig. ♀, Astove Island, Seychelle Islands, R.V. Manihine, Cr.312, 20 August 1970, reef flat, under dead coral, coll. A.J. Bruce. QMW21443, 3  $\delta$ , 3 ovig. ♀ Farquhar Island, Seychelle Islands, R.V. Manihine, Cr.336, stn AJB/60, 26 February 1972, coll. A.J. Bruce. QMW21444, 2 spms (1 ovig. ♀), stn AJB/107, Ras Iwatine, Mombasa, Kenya, 4°01.3'S 39°44.0'E, 1m, 27 February 1971, lagoon, in *Silyphora*, coll. A.J. Bruce. QMW21445, 1 spm ( $\delta$ ?), stn AJB/99, Ras Iwatine, Mombasa, Kenya, 4°04.0'S 39°44.2'E, 0.5m, 1 January 1971, lagoon, in *Pocillopora*, coll. A.J. Bruce. QMW21446, 1 ovig. ♀, stn AJB/157, Jadini, Kenya, 4°19.0'S 39°35.5'E, 2.0m, 19 March 1972, in corals, coll. A.J. Bruce. QMW21447, 1  $\delta$ , 1 ovig. ♀, stn AJB/166, Bamburi, Mombasa, Kenya, 4°00.5'S 39°45.0'E, outer reef crest, 18 August 1973, coll. A.J. Bruce. QMW21448, 1 ♀, 2 juvs, stn AJB/119, Ras Iwatine, Kenya, 4°01.15'S 39°43.8'E, 2m, 27 July 1971, edge of deep reef channel, in *Pavona*, coll. A.J. Bruce. QMW21449, 1 ♀, stn AJB/138, Jadini, Kenya, 4°21.5'S 39°34.5'E, 0-2m, outer lagoon, in coral, 3 November 1971, coll. A.J. Bruce. (author's collection), 1 spm, stn AJB/181a,

Tamarind, Mauritius, intertidal pools, 24 May 1974, coll. A.J. Bruce. QMW21540, 1  $\delta$ , 3 ovig. ♀, stn AJB/140, Vipingo, Kenya, 6 November 1971, reef flat, coll. A.J. Bruce. (author's collection), 2 spms, stn AJB/209, South Patch, Motupore Island, Papua New Guinea, 9°34.27'S 147°12.65'E, 10-20m, seaward reef slope, scuba, 6 November 1980, coll. J.M. Lowry. QMW21451, 1 ovig. ♀, stn AJB/141, Tutia Reef, Mafia Island, Tanganyika, 2m, 14 November 1971, coll. A.J. Bruce. NTMCr.009156, 1  $\delta$ , stn RH 92 12, Cartier Reef, Western Australia, 12°32.6'S 123°32.2'E, 10-15m, 9 May 1992, coll. J.R. Hanley, B.C. Russell. NTMCr.004374, 1  $\delta$ , 1 ovig. ♀, 2 juv., Maausi Bay, Tutuila, American Samoa, reef pool, 0.4m, 22 July 1986, 'Operation Raleigh', coll. M. Richmond. NTMCr.004375, 1  $\delta$ , Omutu Landing, Mitiaro, Cook Islands, reef lagoon, 2-3m, 11 July 1986, 'Operation Raleigh', coll. M. Richmond. NTMCr.004376, 1 ovig. ♀, Oholei, Tongatapu, Tonga, reef lagoon, 1m, 14 August 1986, 'Operation Raleigh', coll. M. Richmond. MNHNna-6627, 2 ♀ (1 ovig.), stn S-20, Tahiti, Society Islands, coll. O. Odineiz, 1982.

**DESCRIPTION.** Small hippolytid shrimp of moderately slender, subcylindrical body form. Carapace smooth, with short acute rostrum, reaching to midlength of proximal segment of antennular peduncle in dorsal view, without distinct dorsal carina, with single small acute tooth at about level of tip of inferior orbital angle in lateral view, ventral carina shallow, concave, lateral carinae broadly divergent, continuous with supraorbital margin, giving rostrum triangular appearance in dorsal view, with small acute supraorbital teeth, posterior to level of dorsal tooth; inferior orbital angle slightly produced, rounded, with small acute antennal spine ventrolaterally; hepatic and pterygostomial spines absent, branchiostegite with anterolateral angle broadly rounded.

Abdomen smooth, with 3rd segment slightly produced posterodorsally, non-carinate; 6th segment c. 1.33 times longer than maximal depth, c. 0.7 of carapace length in  $\delta$ , 0.55 in ♀, with posterolateral and posteroventral angles acute, posteroventral angle non-articulate; first 3 pleura broadly rounded, not markedly enlarged in ovigerous ♀♀, 4th and 5th posteriorly produced, posteroventral angles broadly acute.

Telson c. 1.5 times length of 6th abdominal segment in  $\delta$ , 1.3 times in ♀, subequal to carapace length in  $\delta$ , c. 0.75 in ♀, 2.6 times longer than anterior width, lateral margins sublinear, posteriorly convergent, posterior margin angular with acute median process, with 3 pairs of small dorsal spines at 0.4, 0.6 and 0.8 of telson length, posterior margin with 3 pairs of spines, lateral spines small, subequal to dorsal spines, interme-

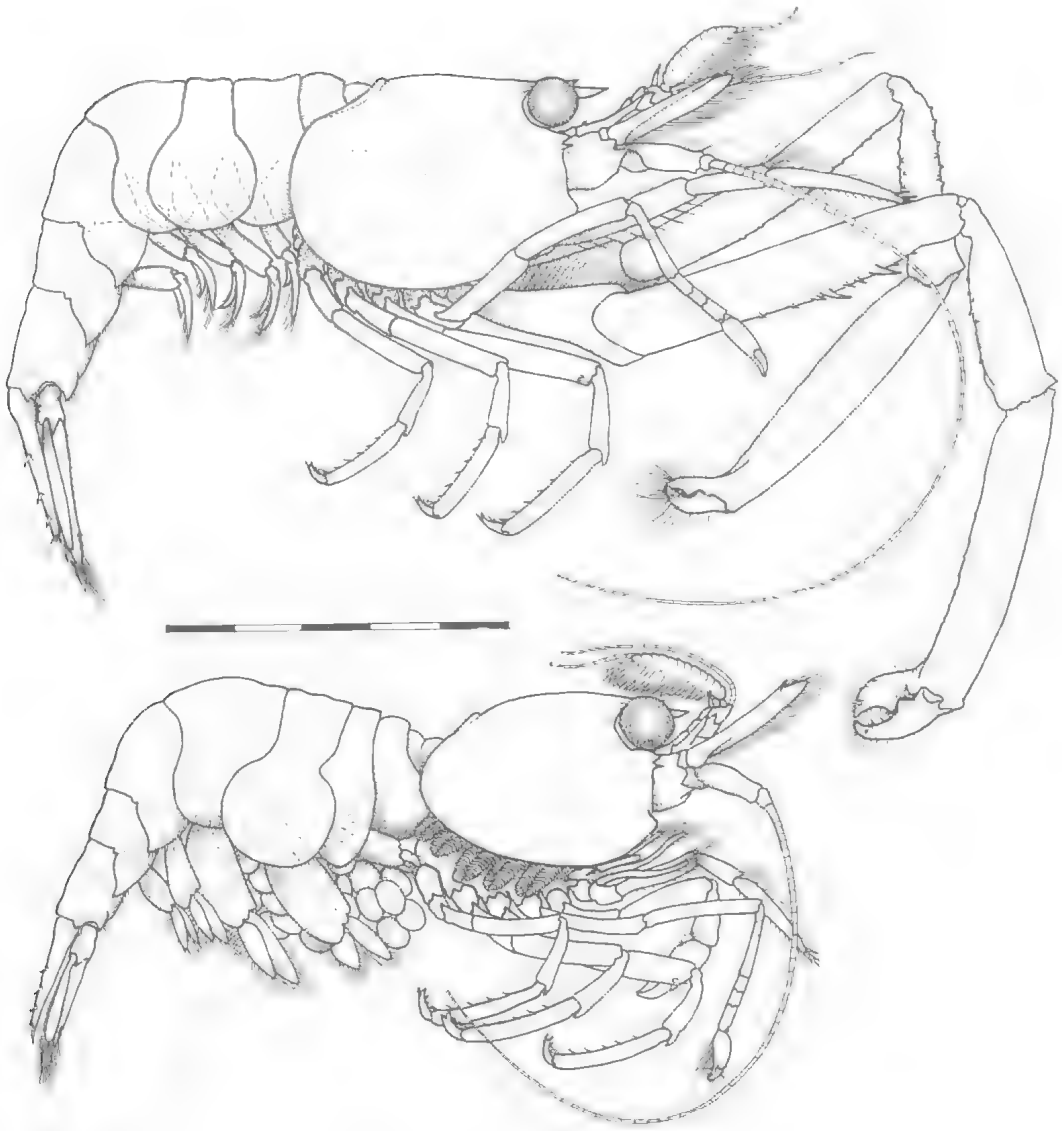


FIG. 1. *Thorina maldivensis* (Borradaile). ♂, Aldabra Island (upper) and ovigerous ♀, Heron Island (lower). Scale in mm.

diate spines c. 3.0 times as long as lateral spines, submedian spines slender, plumose, twice length of lateral spines.

Antennule with proximal segment broad, about as wide as long, with stout acute tooth at 0.6 of ventromedial margin, stylocerite elongate, acute, exceeding length of peduncle, with small anteroverted process proximodorsally; statocyst obsolete; intermediate segment short, broad, with acute non-articulated lateral process; distal seg-

ment short, broad, with articulated triangular plate dorsolaterally; upper flagellum with proximal 12-13 segments stout with dense tufts of aesthetascs dorsolaterally, distal flagellum with c. 5 slender segments; lower flagellum slender, with c. 20 segments.

Antenna with basicerite stout, with broad acute, ventrolateral tooth; carpocerite stout, subcylindrical, extending to about end of antennular peduncle, flagellum short, filiform c. 3.5 times

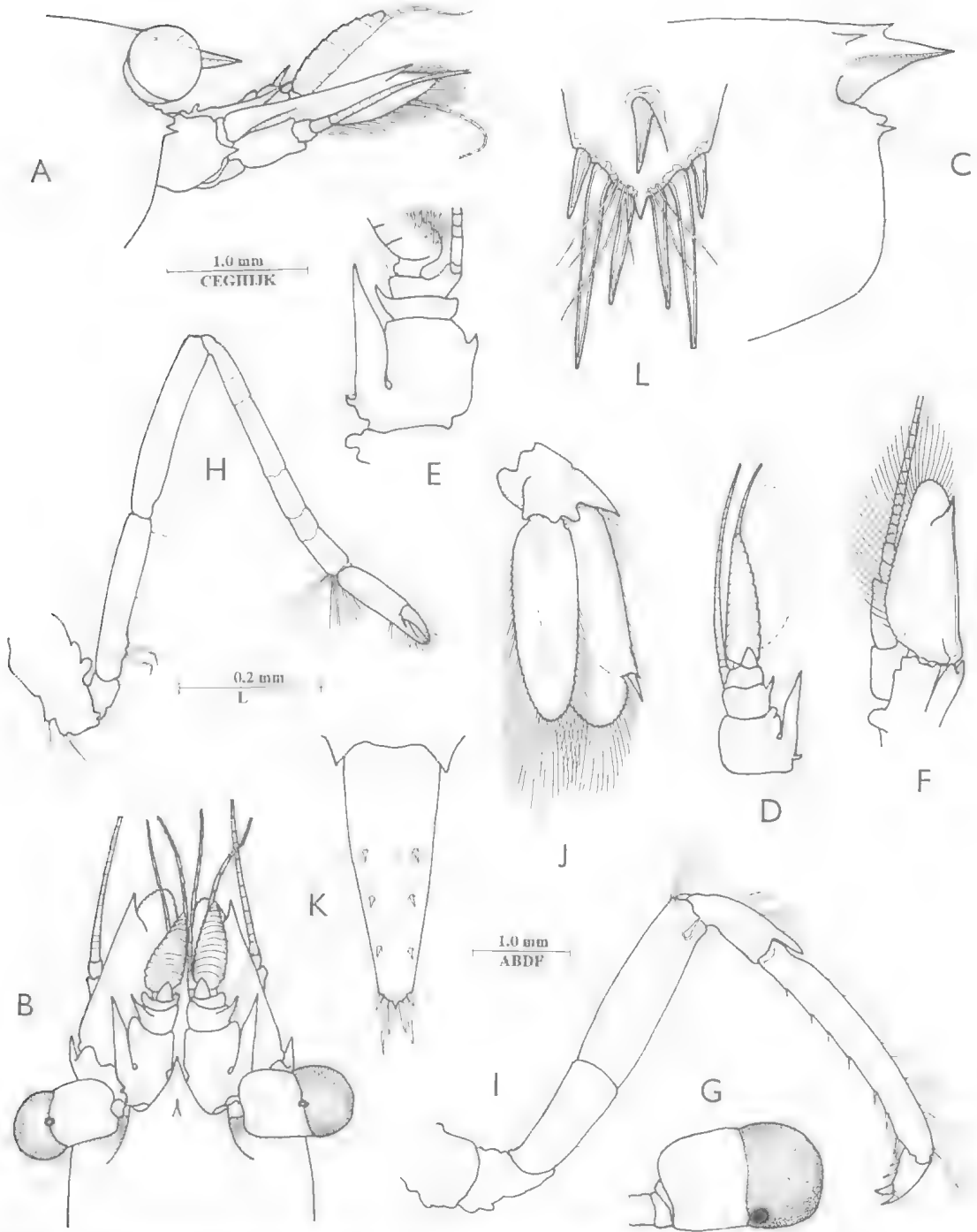


FIG. 2. *Thorina maldivensis* (Borradaile). Ovigerous ♀. Heron Island. A. anterior carapace and appendages, lateral; B. same, dorsal; C. rostrum and anterior carapace, lateral; D. antennule, dorsal; E. same, peduncle, ventral; F. antenna; G. eye, dorsal; H. 2nd pereiopod; I. 3rd pereiopod; J. uropod; K. telson; L. same, posterior spines, dorsal spine (inset).



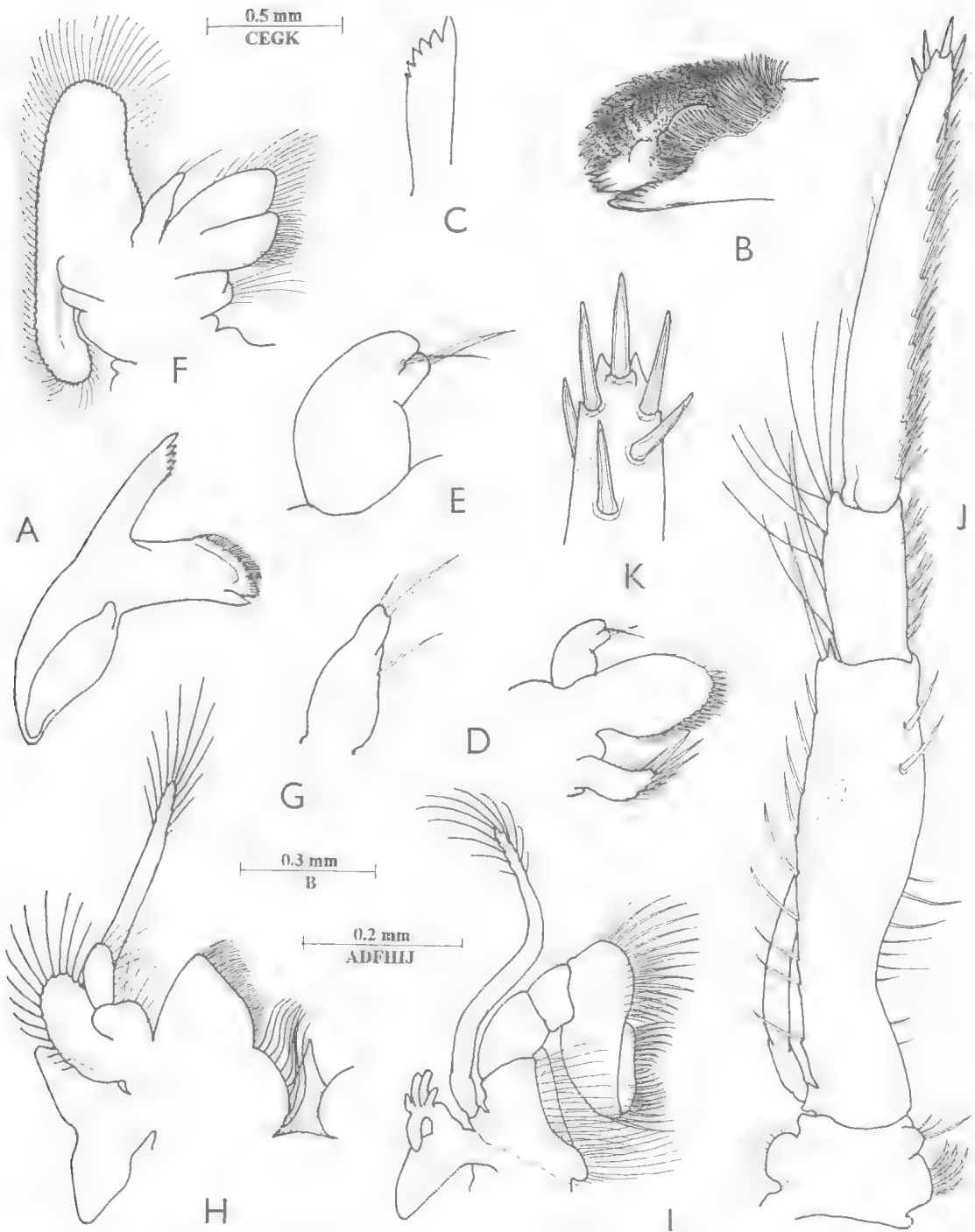


FIG. 3. *Thorina maldivensis* (Borradaile). Ovigerous ♀, Heron Island. A, mandible; B, same, molar process; C, same, incisor process; D, maxillula; E, same, palp; F, maxilla; G, same, palp; H, 1st maxilliped, median process of anterior sternite stippled; I, 2nd maxilliped; J, 3rd maxilliped; K, same, terminal spines of distal segment of endopod.

carapace length. Scaphocerite extending well beyond stout part of upper antennular flagellum, c. 2.5 times longer than maximal width, situated at c. 0.3 of length, tapering distally to rounded distal lamella, distinctly exceeding tip of stout distolateral tooth, situated at c. 0.8 of straight lateral margin length.

Eye well developed, with large well pigmented globular cornea, diameter c. 0.33 of carapace length in male, 0.4 in ♀, with conspicuous dorsal ocellus; stalk stout, compressed.

Mouthparts generally similar to those of *Thor* species. Large acute compressed transverse triangular median plate, anterior to 1st thoracic sternite, occluding space between coxal endites of first maxilliped. Mandible without palp; molar process stout, obliquely truncate distally, with marginal setae and small denticles; incisor process slender, distally oblique, with 6 small acute teeth. Maxillula with short, feebly bilobed palp, upper lobe with slender simple seta, lower lobe with stouter spiniform seta; upper lacinia larger, oval, with numerous short spines distoventrally, lower lacinia small, short, with several long spines distally. Maxilla with slender, tapering palp, with single spiniform terminal seta, short preterminal dorsal seta and medial seta; distal endite well developed, deeply bilobed, densely setose medially; proximal endite feebly developed, slightly bilobed, with few long setae. Scaphognathite well developed, c. 3.0 times longer than central width, posterior lobe small, anterior lobe large, with median margin slightly concave. First maxilliped with 2-segmented palp, distal segment c. 2.5 times longer than wide, sparsely setose medially, proximal segment broader than distal, medial border convex, sparsely setose; basal endite broad, angular, medial margin with dense short setae; coxal endite convex, medial margin with sparse, coarse, long plumose setae; exopod with well developed flagellum with numerous plumose setae distally, caridean lobe small, with numerous plumose marginal setae; epipod large, triangular, feebly trilobed. Second maxilliped with dactylar segment short, narrow, with numerous short stout spines, propodal segment large, broad, distomedial border with numerous long spines; carpus and ischiomerus normal; basis with medial margin excavate, dorsal and ventral medial borders with numerous long slender setae, exopod normal, coxa medially produced, laterally with small elongate epipod, bearing small podobranch anteriorly. Third maxilliped robust, exceeding carapocerite by about terminal and half penultimate

segment in ♂ and terminal segment only in ♀. In ♀, terminal segment c. 7.5 times longer than central width, subcylindrical, slightly flattened ventrally with numerous transverse rows of short spines, distally obliquely truncate, with 6 stout spines; penultimate segment c. 0.3 of terminal segment length, twice as long as wide, with groups of short spiniform setae medially, long setae laterally; ischiomerus segment fused with basis, combined segment subequal to terminal segment length, moderately bowed, compressed proximally, expanded distally, lateral margin with c. 9 spiniform setae, distolateral angle with single long straight spine with short acute tooth medially; basis short, c. 0.2 of antepenultimate segment length, medial margin slightly bilobed, lateral border with small robust rounded epipod; without arthrobranch. ♂ third maxilliped similar to ♀, exceeding carapocerite by penultimate and terminal segments.

First pereopods showing marked sexual dimorphism, small in ♀♀, greatly hypertrophied in some ♂♂. In ♀♀, exceeding basicerite by about carpus and chela; chela c. 0.5 of carapace length, with palm subcylindrical, slightly swollen proximally, with few short pectinate cleaning setae proximoventrally, feebly compressed distally, c. 2.4 times longer than proximal depth, smooth, fingers about 1/2 palm length, stout, tapering distally, with sharp medial cutting edges, dactyl with 4 stout non-cornified terminal teeth, fixed finger with 3, central tooth enlarged with laminar lateral expansion; carpus c. 0.4 of chela length, 2.5 times longer than distal width, tapered proximally, smooth, unarmed, with several cleaning setae distoventrally; merus c. 0.95 of chela length, widest at midlength, 2.8 times longer than central width, with acute ventrolateral tooth distally, proximal ventral margin with single small spiniferous tubercle; ischium c. 0.55 of chela length, compressed, 2.2 times longer than wide, slightly broader distally than proximally, with single small preterminal distoventral spinule; basis and coxa without special features; without exopod. Hypertrophic male chelae slightly unequal, similar, c. 0.25 of carapace length, with palm subcylindrical, without cleaning setae proximoventrally, subuniform, c. 5.5 times longer than central depth, ventromedially tuberculate, fingers c. 0.3 of palm length, stout, deflexed, with numerous long stiff setae, tapering distally, with sharp strongly concave cutting edges, with stout hooked tips crossing distally, dactylus with single large acute tooth proximally, fixed finger with smaller acute tooth more distally; carpus c. 0.5 of

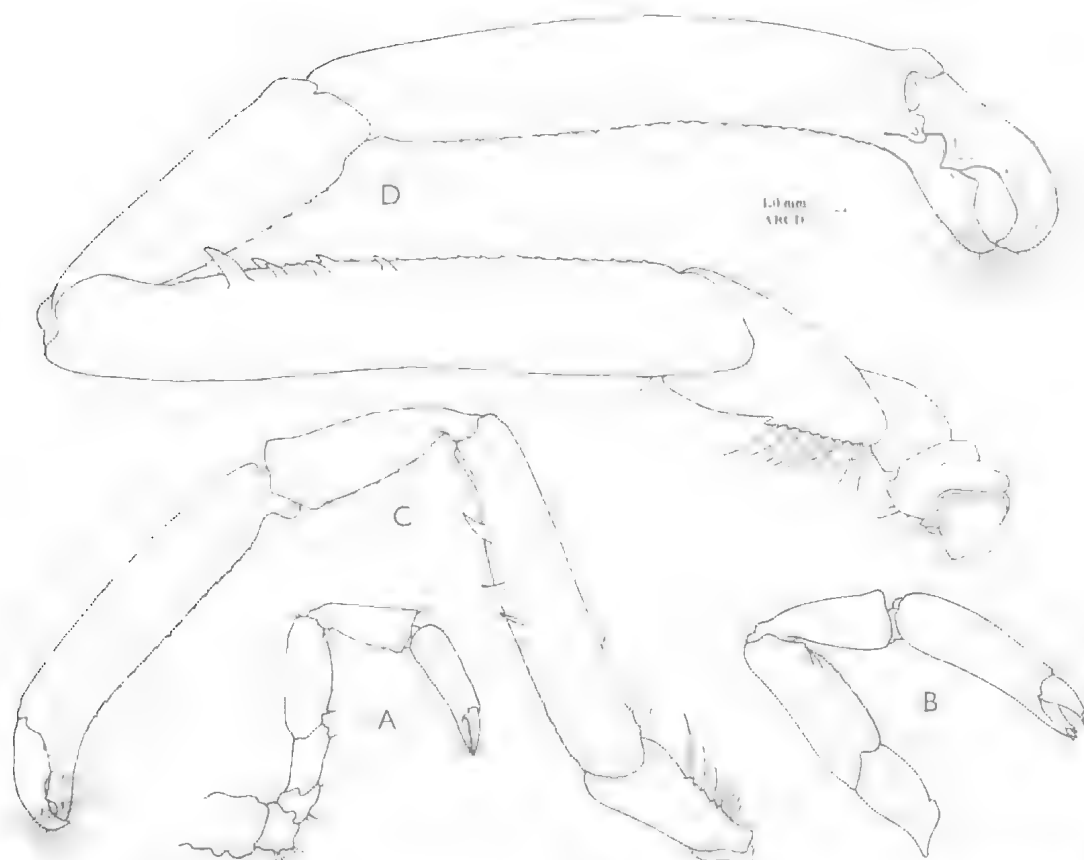


FIG. 4. *Thormia maldivensis* (Borradaile). First pereopods. A, ovigerous ♀, Heron Island, CL 2.2 mm; B, ♂, Heron Island, CL 2.3 mm; C, ♂, Aldabra Island, CL 2.2 mm; D, ♂, Astove Island, CL 2.4 mm.

chela length, 3.3 times longer than distal width, tapered proximally, feebly tuberculate ventromedially, unarmed, without cleaning setae distoventrally; merus c. 0.9 of chela length, subcylindrical, 6.0 times longer than central width, ventrolateral surface tuberculate, with numerous small acute distally directed tubercles, with several (3-6) large stout acute preterminal teeth distolaterally, distoventral angle rounded; ischium obliquely articulated with merus, c. 0.27 of chela length, compressed, distally expanded, 2.0 times longer than greatest width, dorsally carinate proximally with c. 8-9 denticles or tubercles and long stiff erect spiniform setae; basis and coxa robust, without special features; without exopod. Intermediate males with similar but smaller and less robust chelae, less spinose and tuberculate, more closely resembling ♀ chelae.

Second pereopods slender, exceeding caropocerite by carpus and chela in ♀, by chela and 3 distal segments of carpus in ♂, chela with palm

subcylindrical, c. 2.3 times longer than central width, with few setal tufts distally, fingers c. 0.6 of palm length, slender tapering, 3.0 times longer than proximal depth, cutting edges sharp, medial, tips with 3 acute spines on dactyl, 2 spines and short tooth on fixed finger; carpus 2.5 times chela length, 12 times longer than wide, 6-segmented, segments in ratio of 2: 1: 3.4: 1.9: 1.1: 1.6, first 2 segments poorly separated, distal segment with transverse row of long serrulate setae distoventrally, merus c. 1.75 times chela length, 6.3 times longer than central width, 6.0 times longer than wide, simple; ischium 0.9 of merus length, 5.3 times longer than wide, with 2 long simple spiniform setae proximoventrally; basis and coxa without special features.

Ambulatory pereopods moderately robust, third pereopods with slight sexual dimorphism. ♀ third pereopod exceeding caropocerite by propod and dactyl; dactyl c. 0.27 of propod length, 2.6 times longer than proximal depth, stout, com-

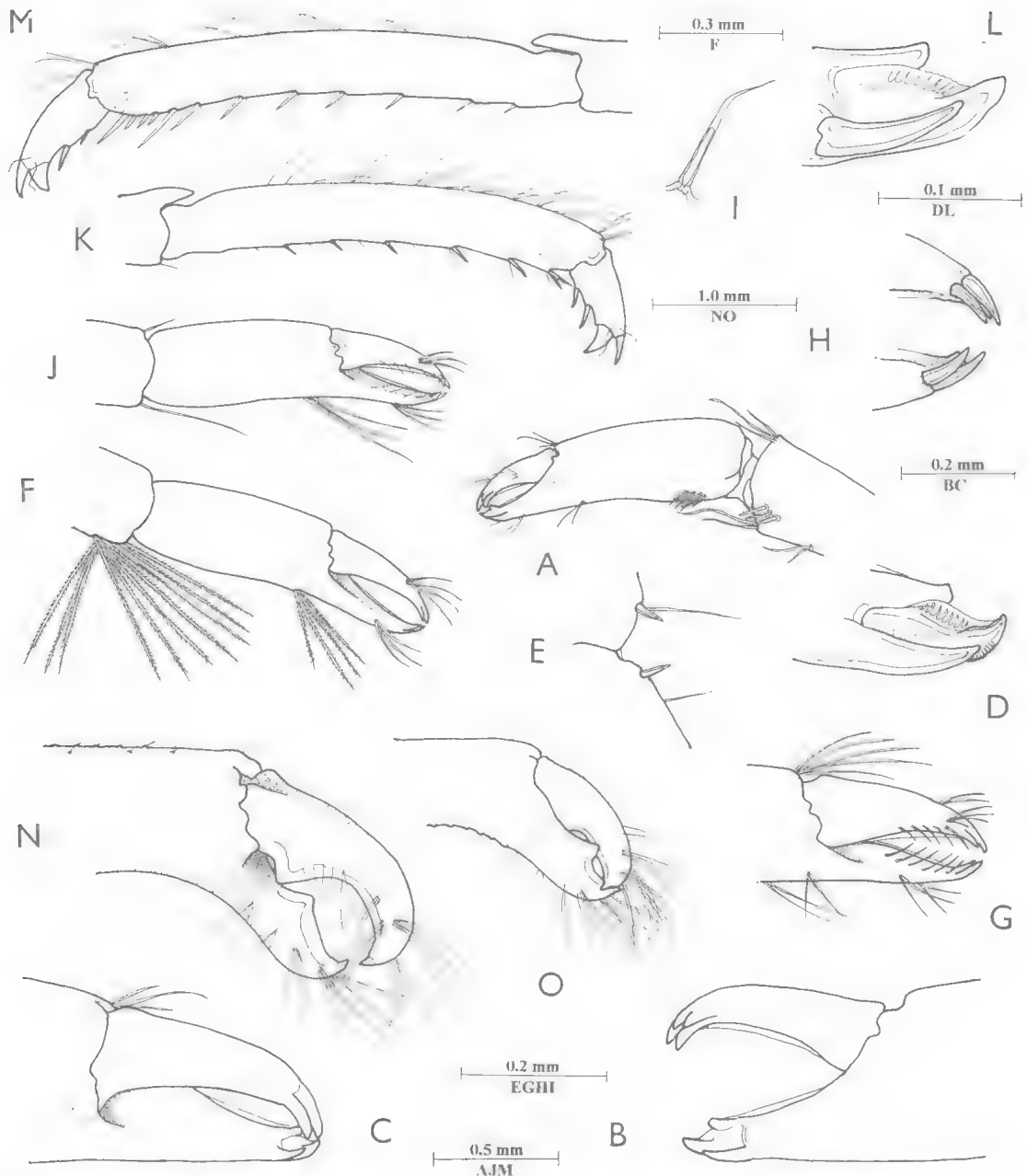


FIG. 5. *Thorina maldivensis* (Borradaile). Ovigerous ♀, Heron Island. A, first pereopod chela and distal carpus; B, fingers of chela, lateral; C, same, medial; D, same, tip of fixed finger; E, same, medial ischiomeral spines; F, 2nd pereopod, chela; G, same, fingers; H, same, distal fingers, dactyl above; I, same, medial ischial spine; J, 2nd pereopod, chela. K, third pereopod, propod and dactyl. ♂, Heron Island. M, 3rd pereopod, propod and dactyl. N, major 2nd pereopod, fingers. O, minor 2nd pereopod, same.

pressed, distal end c. 0.6 of proximal depth, with smaller dorsal unguis and larger, stouter distoventral spine, each c. 0.3 of length of dorsal border of corpus, ventral margin with two spines;

propod c. 0.8 of carapace length, 7.5 times longer than wide, uniform, slightly bowed, ventral border with 2 larger distoventral spines, 5 ventral spines, decreasing in size proximally, dorsal mar-

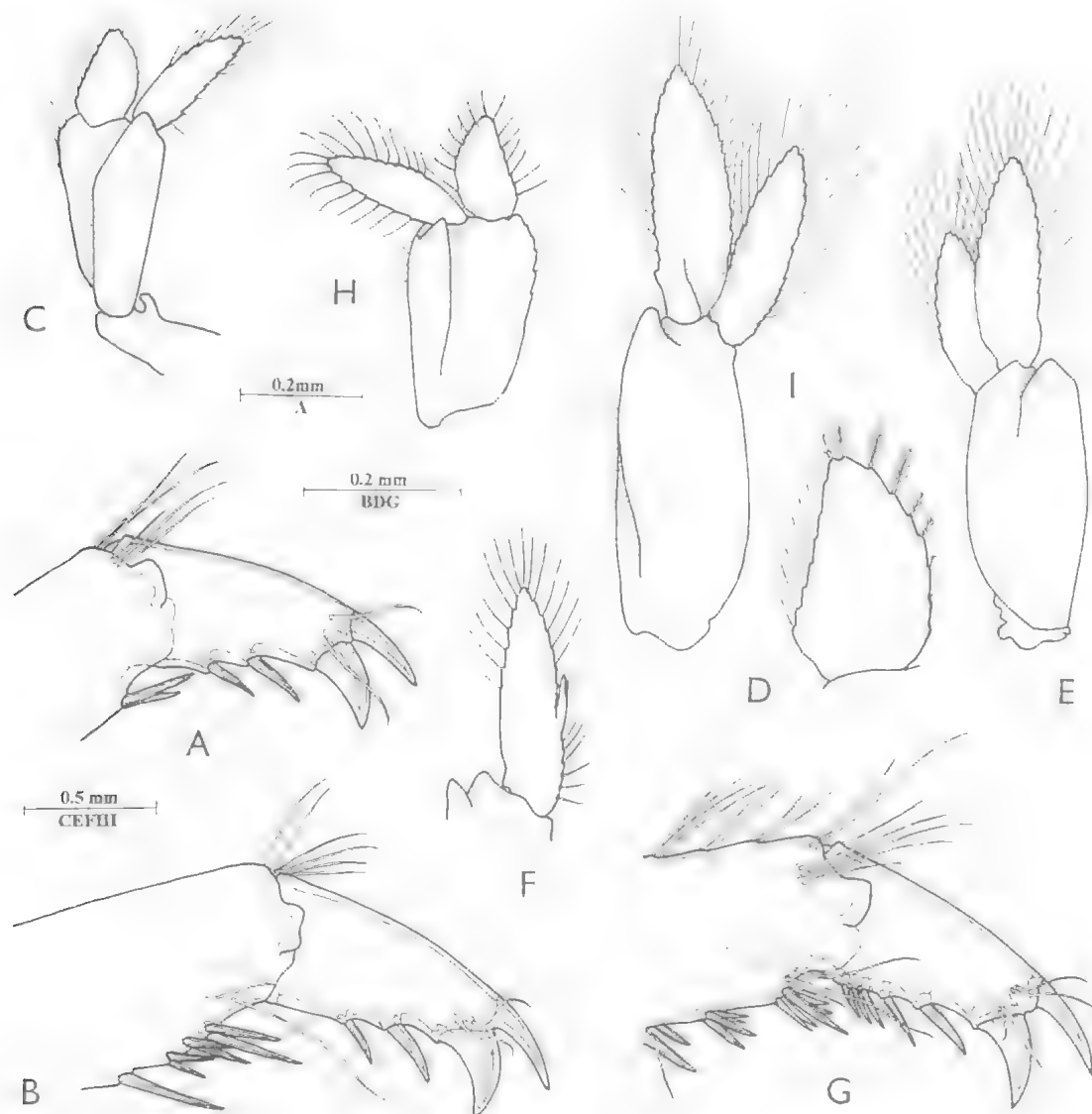


FIG. 6. *Thorina maldivensis* (Borradaile). Ovigerous ♀, Heron Island. A, 3rd pereopod, dactyl. ♂, CL 2.3mm, Heron Island. B, 3rd pereopod, dactyl. C, 1st pleopod. D, same, endopod. E, 2nd pleopod. F, 3rd pleopod, endopod. ♂, CL 2.4mm, Aldabra Island. G, 3rd pereopod, dactyl. H, 1st pleopod. I, 2nd pleopod.

gin sparsely setose; carpus c. 0.36 of propod length, unarmed; merus robust, c. 0.72 of propod length, 3.2 times longer than central width, with articulated distolateral spine; ischium c. 0.68 of meral length, 2.5 times longer than distal width, narrower proximally, unarmed; basis and coxa robust, without special features; without exopod. 4th and 5th pereopods similar to 3rd, propods slightly longer than 3rd pereopod propod length, meri shorter and more slender, 4th c. 0.95 and 5th

0.85 of 3rd merus length. Male 3rd pereopod exceeding carpocerite by propod and dactyl, with slight sexual dimorphism; propod slightly expanded distally in smaller specimen, with 3 pairs of distoventral spines, dactylus as in ♀, with 2 ventral spines; in larger ♂, propod scarcely expanded distally, with 2 groups of 4 and 5 distoventral spines, dactylus with 3 additional spines on proximal ventral margin.



Ovigerous ♀ pleopods without special features, basipodite enlarged and expanded, rami short, broadly expanded, 2nd to 5th endopods with appendix interna. Male 1st pleopod with basipodite robust, broad, ventromedially concave, coxopodite with uncinate distoventral process; endopod sub lanceolate, c. 0.8 of exopod length, 1.6 times longer than proximal width, medial margin straight, setose, lateral margin convex, with short plumose setae; exopod c. 3.3 times longer than wide, with plumose marginal setae; 2nd pleopod larger, endopod c. 0.8 of exopod length, with plumose marginal setae, lacking appendix masculina and appendix interna, exopod normal; third pleopod normal, with appendix interna at c. 0.4 of medial margin length.

Uropod with protopodite with large acute lateral tooth; exopod c. 2.5 times longer than wide, lateral margin straight, sparsely setose, with small acute distal tooth, with large mobile spine medially; endopod 0.95 of exopod length, 3.0 times longer than wide.

**TYPES.** The type material is deposited in the collection of the Zoology Museum, Cambridge, United Kingdom. 3 lots of specimens are held (pers. comm., R.C. Preece, 16 August 1995), consisting of the following: (i) 1 specimen in reasonable condition, from Minikoi, Laccadive Islands; (ii) 1 specimen in reasonable condition, from Salomon Island. (iii) 2 specimens, with loose appendages, from Holulé Island, Malé, Maldives. 2 lots of specimens, (i) and (iii), are noted as co-types. The specimens from Minikoi and Holulé, are noted on their record cards with 'Gardiner Colln. Ann. Mag. Nat. Hist. (8) XX, p. 208. Percy Sladen Trust. Exp. XXII pt 3, p 400'. The Salomon Island specimen is annotated only 'Gardiner Colln.' All have the accession number AR 3.1920.

**MEASUREMENTS** (mm). ♂, Astove Island: postorbital carapace length, 2.3; carapace and rostrum, 3.3; total body length, 12.5; major first pereopod chela, 5.5; minor first pereopod chela, 4.8; 3rd pereopod propod, 1.8; same, merus, 2.3. Ovigerous ♀, Heron Island: postorbital carapace length, 2.2; carapace and rostrum 3.1; total body length, 11.8; 1st pereopod chela, 1.2, 3rd pereopod propod, 1.7; same, merus, 1.9.

**COLOURATION.** The Jadini, Kenya, specimen was noted to be an opaque white, except for the transparent posterior 4th, 5th and 6th abdominal segments and caudal fan; pereopod bases also white, meri banded with white; antennule and

antenna white, filiform flagella transparent. The Mitiaro specimens were noted by the collector as 'translucent, with pink and white mottled head and legs, green tinge to lower abdomen and tail' and 'translucent, with pink predominating, mottled white head and legs', the Tutuila specimens as 'transparent, with green tinge on lower abdomen, mottled green-pink head and legs', and the Tongatapu specimens as 'transparent, with pink tinge and pink mouthparts, red/white eggs, dark body organs'. A good colour photograph is provided by Kamizake et al. (1988). This shows a semi-translucent pale yellowish shrimp, heavily mottled with fine red speckling and scattered whitish patches, particularly at bases of pleopods and base and tips of caudal fan.

**REMARKS.** The exact habitat of *Thorina maldivensis* has not been established but most personally collected specimens have been obtained from shallow intertidal coral reef pools with a wide variety of corals and other coelenterates and algae. As many were collected by the use of poison, the precise niches occupied were not observed. Several specimens were collected from coral heads but these associations may have been accidental. Hayashi (1986) records this species from under coral blocks. The species appears to be generally uncommon, but Edmondson (1946) reported that in Hawaiian waters the species 'is common among brown seaweeds near the shore'. The colouration of the Jadini specimen does not appear cryptic and suggests a commensal lifestyle. Where several specimens were collected together the association is more likely to be genuine. The Papua New Guinea specimens from 10-20m represent the maximum bathymetric range for this species.

The ♂ specimen from Cartier Reef had only un-hypertrophied first pereopods but the distal propod and dactylus of the 3rd pereopods were distinctly sub-prehensile, the ventral dactylus with accessory spines. The ♂ from Tutuila possessed only part of a single first pereopod, lacking the chela. The merus was rather feebly spinulate, with blunt spines, and the spiniform setae along the dorsal margin of the carpus were feebly developed, mostly short and slender, with only a single distal long spiniform seta.

The transverse triangular median sternal process that appears to lie anteriorly to the sternite of the first maxilliped appears unusual but it is rather difficult to discern its exact relationships. No similar feature seems to have been reported in other hippolytids but a similar, though much

smaller and narrower process, more antero-posteriorly orientated, is also present in *Thoramboinensis* (De Man).

**DISTRIBUTION.** Throughout most of the Indo-West Pacific region. Type localities: Malé Atoll, Maldive Islands; Minikoi, Laccadive Islands, and Salomon Island. Also known from Kenya, Tanganyika\*, Mauritius\*, Seychelle Islands\*, Maldive Islands, Andaman Islands, Cartier Reef\*, Great Barrier Reef\*, Papua New Guinea\*, Ryukyu Islands, Marianas Islands, Marshall Islands, Tonga\*, Cook Islands\*, Kiribati, Society Islands\*, and Hawaiian Islands. (\*= new localities). Tanganyika is used in its zoogeographical meaning and not in a political sense.

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**NEW DATA ON *LERISTA INGRAMI*, A RARE SKINK FROM SOUTHERN CAPE YORK PENINSULA, AUSTRALIA.** *Memoirs of the Queensland Museum* 42(1): 24, 1997. - *Lerista ingrami* Storr, 1991 is poorly known. It is treated as 'rare' (McDonald et al., 1991) and was known, prior to Sept., 1996, from 10 specimens (the holotype and nine paratypes) from what amounts to a single locality — the foredune of the beach between the mouth of the Melvor R. and Cape Flattery, on southern Cape York Peninsula. *L. ingrami* is one of a few species of Australian skinks (4/320 species) not photographed in life. The type locality of this species has been visited recently (13 Sept., 1996). As a result, we can clarify some minor discrepancies with collection data of the type specimens; present photographs of a live specimen of *L. ingrami* and of its type locality; describe the colour of *L. ingrami* in life; and comment on prey of *L. ingrami*.

Published data on the type locality and the collection locality of the paratypes of *L. ingrami* is at variance slightly with information recorded in the Queensland Museum register. Storr (1991) records:

'Holotype J32396 in Queensland Museum collected on 27 July 1976 by G.J. Ingram near beach north of Melvor River, Queensland, in 15°07'S, 145°15'E'.

'Paratypes Queensland: 7 km N of mouth of Melvor River (QM20644-51) and 5 km N (QM20653)'.

The QM register entries for these specimens are:

'QMJ32396 (holotype) on mission road near beach, north of Melvor R., 13 July, 1976, G.J. Ingram'. (Date of registration and entry 27 July, 1976).

'QMJ20644-51 (paratypes) approx. 4 km N of Melvor R. mouth, Cooktown 1:250000 428089, 20 Nov., 1970, JAC, T.P. Tebbel, C. Tanner; 'buried in sand under log on first dune'.

'QMJ20653 (paratype) approx. 3 km N of Melvor R. mouth, Cooktown 1:250000 318090, 20 Nov., 1970, JAC, T.P. Tebbel, C. Tanner; 'buried in sand of first dune - under logs'. (Date of registration and entry 6 Jan., 1971).

For the last-mentioned, sometime in or about 1986, latitude/longitude were calculated from an atlas and added to the register in pencil, 15°05'S 145°14'E.

Following advice from G.J. Ingram (collector of the holotype of *L. ingrami*) and using a 'Magellan Global Positioning System (GPS)', we have calculated the type locality for *L. ingrami* (Fig. 1) at 15°07'01"S 145°14'42"E, very close to the locality calculated for/by Storr (but not entered in the QM register) at the time of his description of the species - 15°07' 145°15'.

We collected topotypic specimens QMJ62430-1, QMJ62443. One has been photographed (Fig. 2). All were found in the middle of the day, 'at rest', on slightly moist sand under dead coconuts. Once disturbed, they invariably sought escape into the sand. Both mid body (20 x) and supraciliary



FIG. 2. *Lerista ingrami*. (Photograph, Jeff Wright, QM)

counts (5x2, 4x1) for these specimens fall within the range given for the species by Storr (1991).

*L. ingrami* was described from old (15-21 years) spirit material, so its colour in life was not known. Storr's description (1991) can be augmented: body upper surface a shiny pink or grey-beige, profusely marked by tiny dark brown dots; head scales dark-edged. A sharp-edged dark brown lateral stripe runs from the rostral to the base of the tail, tapering posteriorly. Upper surfaces of limbs the same colour as dorsum, also with dark brown (minute) dots. Venter (SV) pale grey-white. Tail pale to very bright orange ventrally and dorsally.

There is little information on the prey of *Lerista* spp. Wilson & Knowles (1988) report: '... Small arthropods, their eggs and larvae probably constitute the bulk of their diets ...'. *L. bipes* and *L. muelleri* are the only species from sandy localities for which prey have been reported, and there is only one other reference to prey of *Lerista* (a Tasmanian record of Hower & Mollison, 1974). Smith (1976) records orthopterans from *L. bipes*, and proturans and collembolans from *L. muelleri*. Faecal pellets from the recently-collected *L. ingrami* have been examined by Dr G. Monteith, Senior Curator (Entomology) at the Queensland Museum. They contain remains of two small scorpions (Arachnida: Scorpionida) and two small seed bugs (Insecta: Lygaeidae). Both, he advises, are common and active amongst leaf litter.

Tissue samples were taken from QMJ62430 and QMJ62431 and sent to the tissue library of the South Australian Museum, Adelaide. Only minor external morphological characters (e.g., mid-body scales, lamellae of the third toe, supraciliary scales and colour) separate *L. ingrami* from *L. orientalis* (De Vis, 1889) and *L. zonulata* Storr, 1991.

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FIG. 1. The type locality of *Lerista ingrami* Storr, 1991. (Photograph, JAC)

TWO NEW SPECIES OF FRESHWATER ATYID SHRIMPS (CRUSTACEA: DECAPODA: ATYIDAE) FROM NORTHERN QUEENSLAND AND THE DISTRIBUTIONAL ECOLOGY OF THE *CARIDINA TYPUS* SPECIES-GROUP IN AUSTRALIA

SATISH CHOY AND JONATHAN MARSHALL

Choy, S. & Marshall, J. 1997 06 30: Two new species of freshwater atyid shrimps (Crustacea: Decapoda: Atyidae) from northern Queensland and the distributional ecology of the *Caridina typus* species-group in Australia. *Memoirs of the Queensland Museum* 41(1): 25-36. Brisbane. ISSN 0079-8835.

Two new species of freshwater atyid shrimps are described from tropical Queensland and the four members of the *Caridina typus*-group now known from Australia are reviewed. *Caridina confusa* sp. nov. is a slender animal with a relatively long, dorsoventrally flattened, naked rostrum, found predominantly in open grassland streams of the Atherton Tableland. *Caridina spinula* sp. nov., distinguished by its spiniform pterygostomian angle, is found in small secondary rainforest streams on northeastern Cape York Peninsula. Although both these new species look superficially like *C. zebra* Short, 1993, they can be distinguished by a combination of characteristics such as rostrum length, shape of the pterygostomian angle, length-depth ratio of the sixth abdominal segment and the shape of the protopod of the uropod. *C. zebra* is found predominantly in primary rainforest streams of the Atherton Tableland and *C. typus* is found in coastal tropical streams. All species are allopatric, except for slight overlap in the distribution of *C. zebra* and *C. confusa* in some anthropogenically disturbed streams of the upper Barron and the upper North Johnstone catchments. □  
*Crustacea, Atyidae, Caridina, Queensland, distribution.*

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*Caridina zebra* Short, 1993 is a tropical montane species belonging to the *Caridina typus* species-group (Short, 1993). This group is characterised by a short, dorsally unarmed rostrum, the presence of epipods on the 1st four pairs of pereopods and the presence of an appendix interna on the endopod of the 1st pleopod of ♂♂. Short (1993) reported *C. zebra* from the montane streams of the wet tropical rainforest areas of the Tully, Herbert and Johnstone River catchments, at altitudes of 400-900m. A smaller population of *C. zebra*, is also known to occur in the lower Koolmoon Creek (alt. 150m), a tributary of the Tully River (Hughes *et al.*, 1996). *Caridina typus* Milne Edwards, 1837 has been reported from coastal lowland streams at Cooktown and on Dunk Island (Roux, 1926; Riek, 1953; Short, 1993).

Re-examination of Short's material from the Wet Tropics-Atherton Tableland area (Short, 1993: 62) indicated the presence of two distinct morphological groups, one group possessing a longer rostrum, from anthropogenically disturbed grassland areas and the other possessing a shorter rostrum, generally from relatively undisturbed rainforest areas. This was confirmed by examination of recently collected material from

the same area (17-18°S, 145-146°E). Although the distribution of these two groups tend to overlap slightly, they are morphologically and ecologically distinct. They each warrant species status. Since the short rostrum form is the holotype of *C. zebra* Short, 1993, its status is maintained. The long rostrum form is described as a new species, *Caridina confusa*.

A third morphological and geographically isolated group was recently collected from the streams in the Mellwraith Range, Cape York Peninsula (13°35-44'S, 143°20'E). This is also described as a new species, *Caridina spinula*.

#### MATERIAL AND METHODS

Specimens from the Queensland Museum are provided with catalogue numbers with the prefix QM. Unless otherwise stated all material was collected by the first author and various colleagues from Griffith University and the Queensland Department of Natural Resources (formerly part Department of Primary Industries). All examined specimens will be deposited in the Queensland Museum. Collection was made using a standard pond net and all samples immediately preserved. The abbreviations used are: 6S, sixth abdominal segment length; AIP, antennular pe-

duncle length; A2P, antennal peduncle length; CL, post-orbital carapace length; RL, rostrum length; SC, scaphocerite length; SL, body length from the post-orbital margin of the carapace to the tip of the telson; ST, stylocerite length; T, telson length.

The format of the description and morphological terms follow Choy (1991). Although problems in the terminology of cuticle spination and setation still exist, we have followed the terminology of Felgenhauer (1992).

### SYSTEMATICS

#### *Caridina typus* Milne Edwards, 1837

*Caridina typus* Milne Edwards, 1837, p. 363, pl. 25bis, figs. 4, 5; Holthuis, 1965, p. 10, fig. 3.

*Caridina typus typica* Bouvier, 1925, p. 250, figs. 272-295.

*Caridina typa* Reux, 1926, p. 201; Rick, 1953, p. 117.

**MATERIAL EXAMINED.** Proserpine River below Proserpine (20°24.2'S, 148°31.1'E), 19.10.94, L.K. Patterson, 15 ♂♂ (2.5-4.1mm CL), 7 ♀♀ (4.8-5.1mm CL); QM W4795, Brandy Creek near Proserpine (20°20'S, 148°38'E), 21.4.75, R. Monroe, P. Fillewood, ovigerous ♀ (7.81mm CL), non-ovigerous ♀ (5.82mm CL); QM W14241, Lindeman Is., west side, small creek near golf course (20°27'S, 149°02'E), 27.3.83, J. Short, ♂♂ (4.03-4.09mm CL), ♀♀ (5.5-7.2mm CL).

**DIAGNOSIS.** Rostrum short, laterally compressed, with 1-5 teeth on ventral margin; diaeresis with more than 20 hamate setae; intermediate setae on posterior telsonic margin longer than lateral pair, plumose, with sclerotinous plug; egg small (length <0.52mm).

**REMARKS.** *Caridina typus* has a wide ranging distribution, extending from eastern and southern Africa through the Indian Ocean islands, Southeast Asia to Japan, Australia and through to French Polynesia. In Australia it has been collected only from the northeastern coastal areas of the mainland and from the nearby islands, between latitudes 15-21°S. Although it seems to be confined to the lower reaches of coastal and island Australian streams, *C. typus* has been collected from altitudes of 300m elsewhere (Choy, 1991).

#### *Caridina zebra* Short, 1993

*Caridina zebra* Short, 1993, p. 62 (in part).

**MATERIAL EXAMINED.** All specimens listed by Short, 1993, p. 62. **ADDITIONAL MATERIAL.**

Upper Tully Catchment: QMW17118, Tully River above Koombooloomba Dam (17°49'S, 145°35'E, 720m), 23.10.91, numerous specimens; Koombooloomba Creek (17°51.5'S, 145°35.9'E, 790m), 30.10.93, 25 specimens; Echo Creek (17°59.5'S, 145°38.3'E, 830m), 30.10.93, 50 specimens; Carpenter Creek (17°53.3'S, 145°35.3'E, 750m), 30.10.93, 23 specimens; Costigan Creek (17°56'S, 145°37'E, 770m), 3.12.94, 11 specimens (1.8-4.2mm CL); QMW17119, Koolmoon Creek (17°44'S, 145°34'E), 25.7.90, 4 specimens; Koolmoon Creek at Walter's Waterhole (17°44.11'S, 145°34'E, 760m), 30.10.93, 7 specimens; Koolmoon Creek near Tully River confluence (17°44.9'S, 145°37.1'E, 150m), 31.10.93, 6 specimens; Upper Herbert Catchment: QMW17116, Blunder Creek (17°46'S, 145°33'E), 28.11.90, 3 specimens; Blunder Creek (17°47.5'S, 145°32.2'E, 750m), 3.12.94, 1 ♂, 2 ovigerous ♀♀ (4.08-5.6mm CL); Rocky Creek (17°44.7'S, 145°31.3'E, 760m), 30.10.93, 34 specimens; Cameroon Creek, 3.12.94, 14 specimens (1.4-4.2mm CL); millstream River at Diversion Weir (17°40'S, 145°26'E, 720m), 12.10.94, 2 specimens; Upper North Johnstone Catchment: QMW19261, Malanda Falls, (17°20.2'S, 145°43.8'E, 750m), 2.11.93, 30 specimens (including ovigerous ♀♀); QMW19285, Raspberry Creek, 3-4 km above Malanda Falls (17°22.75'S, 145°33.6'E), 14.11.91, J. Short, P. Davie, A. Humpherys, silt & para grass (*Urochloa mutica*) infested stream; Raspberry Creek (17°25.5'S, 145°28.8'E), 31.10.93, 100 specimens; North Johnstone River (17°40'S, 145°39'E, 650m), 5.8.93, 2 ♀♀, 1 ♂; Ithaca Creek (17°24'S, 145°38'E, 650m), 7.11.94, 2 ♀♀; Ithaca Creek at Bauld Rd (17°23'S, 145°38'E, 685m), 13.10.94, 50 specimens; Thiaki Creek at edge of rainforest (17°25'S, 145°32'E, 795m), 5.12.94, 9 specimens (3.4-4.8mm CL); Thiaki Creek in rainforest, 13.10.94, 15 specimens; North Beatrice River at Palmerston Highway (17°32'S, 145°36'E, 720m), 13.10.94, 25 specimens; Henrietta Creek at Palmerston Highway (17°36'S, 145°45'E, 360m), 14.10.94, 18 specimens; QMW18722, Goolagan Creek, 23.10.91, numerous specimens; Goolagan Creek (17°36.3'S, 145°45.5'E, 370m), 32 specimens; Upper Barron Catchment: QMW3078, Atherton tap water (17°16'S, 145°29'E), 14.5.62, QDPI, 2 ♂♂; Barron River at The Crater (19°17'S, 145°29'E), 7.12.94, 10 ♂♂, 8 ♀♀ (2 ovigerous) (2.0-5.0mm CL); Barron River at Hemmings Road, 28.11.94, 3 juveniles; Wright's Creek (17°04'S, 145°45'E), 4.12.94, 4 ♀♀ (1 ovigerous); Peterson Creek (17°17'S, 145°36'E), 1994-95, numerous specimens; Kauri Creek (16°54'S, 145°38'E), 1994-95, numerous specimens; Prior's Creek, 1 ♀; Upper Gwynne Creek in small pocket of rainforest (17°23.3'S, 145°30.3'E), 5.12.94, 2 ♀♀, 19 ♂♂ (3.6-4.0mm CL).

**DIAGNOSIS.** Body (Fig. 1b) rotund, may have black and white transverse banding; rostrum (Fig. 2a-f) short, extending to base of 3rd antennular peduncle (RL<0.5CL), dorsoventrally com-



FIG. 1. a, *Caridina confusa* sp. nov., ♂; b, *C. zebra* Short 1993, ♂; c, *C. spinula* sp. nov., ♂. Scale = 1 mm.

pressed, may have an apical tooth (Fig. 2e); pterygostomian angle acute but not spiniform; dorsal telsonic spines (Fig. 3a) on posterior 0.66 of telson; posterior telsonic margin (Fig. 3f, g) usually with median spine, sub-lateral pair of setae sigmoid, longer than intermediate setae, setation numerically variable; protopod of uropod (Fig. 3a, d) elongate, spinate; eggs large (length <1.32mm); found mainly in primary rainforest streams on the Atherton Tableland along the Lamb-Francis-Cardwell Ranges.

**REMARKS.** Specimens of *C. zebra* from some locations (streams in the upper Barron Catchment) may seem to have a fairly long rostrum (Fig. 2a, d, f), thus resembling *C. confusa* sp. nov. However, the rostrum length relative to the carapace length as well as other features (Table 2), such as the relative lengths of the antennular peduncle, scaphocerite, sixth abdominal segment and the telson are characteristic of this species. *Caridina zebra* is one of only two species of atyid shrimps in the primary rainforest streams of the upper Tully (the other being *Australatya striolata*), where it is very abundant. In other catchments (Barron, N. Johnstone and Herbert),

it is found mainly in the rainforest reaches of streams. However, it may be common in some disturbed streams such as Raspberry, Ithaca and Prior's Creeks. Unlike the upper Tully, which has an extensive relatively undisturbed forested area, the upper reaches of the Barron and N. Johnstone Rivers have been generally cleared and converted to pasture. Streams running through these open grassland are inhabited predominantly by *C. confusa* sp. nov. Only a small area of the upper Herbert catchment is in the wet (simple notophyll vine to complex mesophyll vine) forest; the rest is in dry sclerophyll forest. The abundance of *C. zebra* in these dry-zone streams is low; these streams are inhabited by another atyid, *Paratya australiensis*. It is interesting to note that only specimens from some of the rainforest streams of the upper Tully have the black and white transverse banding on their bodies (see Short, 1993). In all other areas these animals are translucent brown, with scattered tiny reddish and bluish-green chromatophores, similar to individuals of the two new species.

#### *Caridina confusa* sp. nov.

*Caridina zebra* Short, 1993, p. 62 (in part): QMW18841, QMW18720.

**MATERIAL EXAMINED. HOLOTYPE.** QMW-21906 ovigerous ♀, 4.8mm CL, 2.56mm RL, 19.2mm SL, Thiaki Creek at Seamark Road crossing (17°23.5'S, 145°32.5'E, 750m), stream flowing through open grazing land, fringing para grass, water depth 0.3-0.5m, velocity 0.3ms<sup>-1</sup>, silty substrate, hand-netted amongst edge para grass, 26.8.94, S. Choy, M. Hopper. **ALLOTYPE.** QMW21907 adult ♂, 3.4mm CL, 2.0mm RL, 14.2mm SL, same locality data as holotype. **PARATYPES.** Upper North Johnstone Catchment: QMW21908 upper North Johnstone River near Bromfield Swamp (17°22.5'S, 145°31.3'E, 700m), open grazing land, fringing para grass, water depth 0.3-0.5m, hand-netted, 4.12.94, 21 ♂♂, 50 ♀♀ (13 ovigerous), (2.6-5.0mm CL); QMW18841, Thiaki Creek (17°24.9'S, 145°35.3'E, 750m), water depth 0.2m, electro-fished, 1992, Queensland DPI Fisheries Johnstone Rivers Survey, 1 ♂ (4.5mm CL); QMW18720, small creek about 6 km SW of Malanda (17°22.7'S, 145°33.6'E, 750m), fringing para grass, water depth 0.2-1.5m, electro-fished, 1992, Queensland DPI Fisheries Johnstone Rivers Survey, ♂ (3.9mm CL), 2 ♀♀ (4.3, 4.5mm CL); QMW18725, Thiaki Creek, macrophyte area, same data as QMW18841, 13 ♂♂ (3.2-4.8mm CL), 16 ♀♀ (3.8-6.1mm CL); QMW21909 Thiaki Creek at Seamark Road crossing (17°23.5'S, 145°32.5'E, 750m), open grazing land, fringing para grass, water depth 0.3-0.5m, hand-netted, 26.8.94, c. 100 specimens; QMW21910 Thiaki Creek at downstream edge of rainforest, fring-

ing para grass, depth 0.3-0.5m, hand-netted, 5.12.94, c. 50 spec.; QMW21917 Ithaca Creek in rainforest pocket (17°24.7'S, 145°30.3'E), leaf litter, water depth 0.3-0.5m, hand-netted, 5.12.94, 6 ♂♂, 7 ♀♀ (2 ovigerous). Upper Barron Catchment: QMW21911 Gwynne Creek at Gillies Road crossing (17°20.3'S, 145°31.1'E, 750m), open grazing land with small pocket of riparian rainforest upstream, fringing para grass, water depth 0.3-0.6m, hand-netted, 5.12.94, c. 200 specimens (1.28-5.84mm CL); QMW21912 upper Gwynne Creek in rainforest pocket (17°23.3'S, 145°30.3'E, 720m), hand-netted, leaf litter, water depth 0.2-0.4m, 5.12.94, 14 specimens (4.0-5.4mm CL).

**DIAGNOSIS.** Body slender; rostrum long, reaching tip of antennular peduncle ( $RL > 0.5CL$ ), dorso-ventrally compressed, may be armed with one dorsal tooth; antennular peduncle long ( $A1P > 0.5CL$ ), antennal peduncle long ( $A2P > 0.6CL$ ), stylocerite long ( $ST > 0.4CL$ ), scaphocerite long ( $SC > 0.8CL$ ), sixth abdominal segment long ( $6S > 0.5CL$ ) with acute postero-ventral margin; telson long and slender ( $T > 0.6CL$ ); dorsal telsonic spines confined to posterior half of telson, median spine on posterior telsonic margin absent; protopod of uropods acute but not spinose.

**DESCRIPTION.** Body (Fig. 1a) small, sub-cylindrical; ♂♂ in collection up to 4.9mm CL, ♀♀ up to 6.2mm CL.

Cephalothorax (Figs. 2i, j; 4a, b) rotund, glabrous, breadth c. 0.7 CL, depth c. 0.7 CL; rostrum long, 0.43-0.76 CL, length 12-16 X height, curving downward or sigmoid, reaching base to tip of distal segment of antennular peduncle, asetose, dorsoventrally compressed, a dorsal tooth may be present. Antennal spine short, strong, placed on lower orbital angle; pterygostomian angle obtuse, pterygostomian spine absent. Eyes large, c. 0.25 CL, corneal diameter c. equals eyestalk length, retinal pigmentation present. Antennular peduncle shorter than scaphocerite, 0.6-0.7 CL;

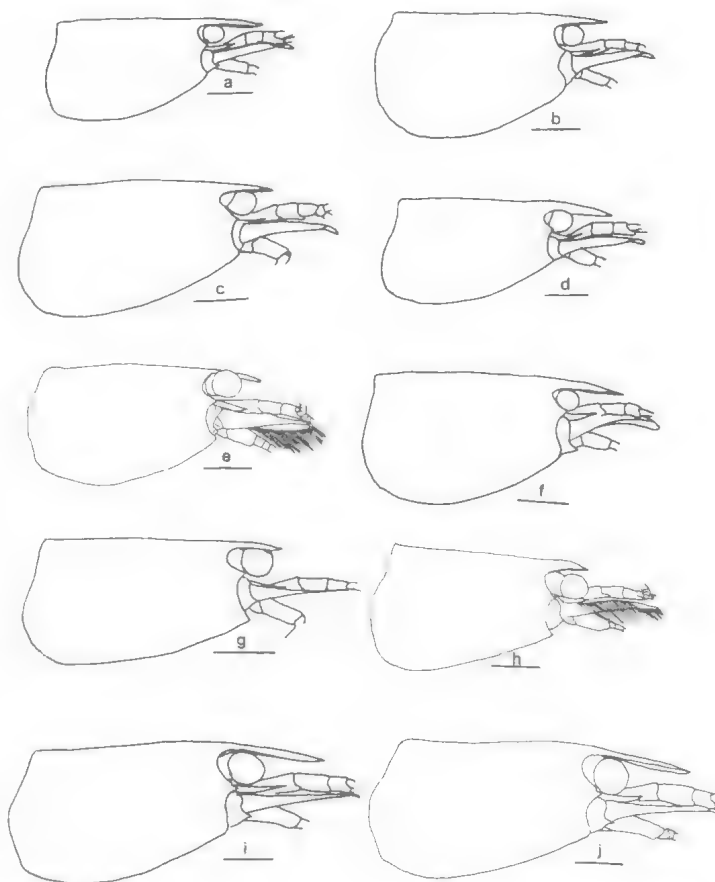


FIG. 2. a, *C. zebra*, from Wright's Ck, ovig. ♀; b, *C. zebra*, from Kauri Ck, ovig. ♀; c, *C. zebra*, from upper Gwynne Ck, ♀; d, *C. zebra*, from Peterson Ck, ♂; e, *C. zebra*, from upper Tully River, ♀; f, *C. zebra*, from upper Gwynne Ck, ♀; g, *C. spinula*, ♀; h, *C. spinula*, ♂; i, *C. confusa*, from Gwynne Ck, ovig. ♀; j, *C. confusa*, from Gwynne Ck, ♂. Scale = 1 mm.

stylocerite length 0.7 X proximal antennular segment length; anterolateral angle of proximal segment acute, reaching to about 0.15 X intermediate segment length; intermediate segment 0.7 X proximal segment length, about 1.7 X distal segment length; all segments with submarginal plumose setae; distal segment fringed laterally and apically with plumose setae. Antennal peduncle 0.5-0.6 X scaphocerite length; scaphocerite slightly longer than antennular peduncle, 0.8-1.0 CL, outer margin straight to slightly concave, asetose, ending in strong subapical spine, length 3.5 X width, distal lamella and inner margin with plumose setae. Branchial formula typical for genus.

Mandibles dimorphic, without palp; right mandible with 6-8 strong, sharp incisor teeth laterally;





FIG. 3. a, *C. zebra*, telson and protopod of uropod, ♂, 4.8mm CL; b, *C. confusa*, telson and protopod, ♂, 4.32mm CL; c, *C. confusa*, posterior body; d, *C. zebra*, posterior body; e, *C. zebra*, dactylus of 3rd pereopod of ♀; f, *C. zebra*, dactylus of 3rd pereopod of ♂; g, h, *C. zebra*, posterior margin of telson. Scales = 1mm (a-d), 0.1mm (e-h).

medially two groups of setae, one group with bent hamate setae, other group with finer straight plumose setae; molar process ridged; left mandible with 6-8 strong teeth; medially three groups of setae, molar process ridged.

Maxillula with simple palp, slightly expanded distally, with long plumose setae distally, few simple setae proximally; lower lacinia with broadly rounded margin, bearing several rows of plumose and simple setae; upper lacinia broadly elongate, inner edge straight, with several rows of strong spiniform, hamate, denticulate and plumose setae, outer and lower inner margins with plumose setae.

Maxilla with slender tapering palp, shorter than upper endite cleft, setose; margin and submargin of upper and middle endite with simple, hamate, plumose and denticulate setae; lower endite with hamate setae; scaphognathite with regular row of long plumose setae on distal margin, with shorter hamate ones continuing down proximal triangu-

lar process which has c. 11 long simple setae, some with prominent dilation at base.

First maxilliped with broadly triangular lamellar palp, ending in pointed tip, margins with plumose setae; ultimate and penultimate segments of endites indistinctly divided; inner margin of ultimate segment with long denticulate setae, long rows of plumose, simple and hamate setae submarginally, transverse rows of plumose setae proximally; exopod flagellum distinct, well-developed, with submarginal and marginal plumose setae; caridean lobe narrow, with marginal and submarginal plumose setae.

Second maxilliped with dactylar and propodal segments of endopod fused; inner margins of all three proximal segments with long simple, hamate and plumose setae; exopod long, narrow with marginal long plumose setae distally and shorter ones proximally.

Third maxilliped reaching beyond tip of antennular peduncle; endopod three-segmented, basal segment length c. 7 X width; penultimate segment length c. 7 X width, c. 0.9 X basal segment length, with transverse rows of spiniform hamate setae; distal segment c. 0.9 X as long as penultimate segment, ending in large claw-like apical hamate seta surrounded by simple and plumose ones, behind which there are 7-9 hamate setae on distal 3rd of posterior margin, clump of serrate and pappose setae proximally; exopod reaching about 0.5 of 2nd endopod segment, distal margin with long plumose setae.

First pereopod (Fig. 4c) reaching tip of basal antennular segment; chela length 1.7-2.2 X width, movable finger 1.1 X as long as palm, length 2.9-3.1 X width; finger tips rounded, without hooks, setal brushes well developed. Carpus attached to chela ventrally, excavated distodorsally, length 1.3-1.6 X width, 0.6-0.8 X chela length, 0.94 X merus length. Merus compressed, 0.6 X as wide as carpus. Ischium length 0.41 X merus length. Epipod present.

Second pereopod (Fig. 4d) reaching tip of 2nd segment of antennular peduncle, more slender and longer than 1st pereopod. Chela length 2.4-2.6 X width; movable finger length 4.9-5.1 X width, 1.5 X as long as palm; finger tips without hooks, setal brushes well developed. Carpus subconical, length 3.5-4.8 X width, 1.0-1.3 X chela length, 1.2 X merus length. Ischium length 0.67 X merus length. Epipod present.

Third pereopod over-reaching antennular peduncle tip by about 0.33 distal propodus. Dactylus sexually dimorphic in adults (cf. Figs. 3e and 3f), length c. 3.8 X width, c. 0.2 X propodus

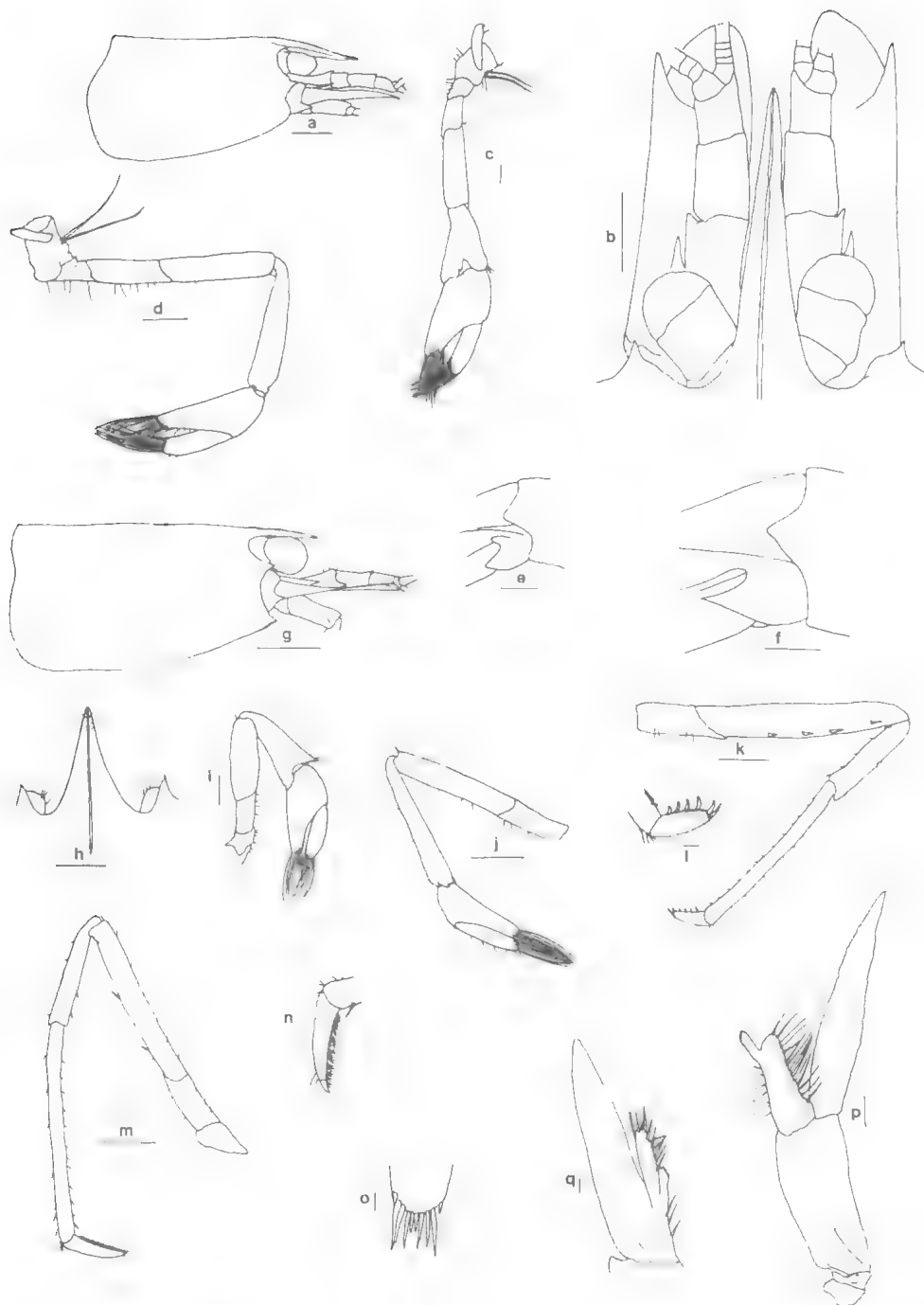


FIG. 4. a-e, *Caridina confusa* sp. nov.: a, cephalothorax; b, anterior cephalothorax, dorsal view; c, 1st pereopod; d, 2nd pereopod; e, margin of abdomen and telson, lateral view; f-q, *C. spinula* sp. nov.: f, margin of abdomen and telson, lateral view; g, cephalothorax; h, rostrum and orbital margin, dorsal view; i, 1st pereopod; j, 2nd pereopod; k, 3rd pereopod; l, dactylus of 3rd pereopod; m, 5th pereopod; n, dactylus of 5th pereopod; o, posterior margin of telson; p, 1st pleopod of adult ♂; q, endopod of 2nd pleopod of adult ♂. Scales = 1 mm (a, g), 0.5 mm (b-f, h-k, m), 0.1 mm (l, n, o-q).

length, ending in prominent claw-like hamate seta surrounded by simple setae, behind which posterior margin bears 4-6 shorter spiniform hamate setae, these being more robust and upright in adult ♂♂. Propodus length 9-11 X width, posterior margin and lateral surface bearing two rows of small spiniform hamate setae. Carpus length 0.8 X propodus length, distal projection feebly developed, posterior and lateral surfaces with up to 10 small hamate setae, more spiniform setation in adult ♂♂. Merus 1.1-1.4 X length of carpus, with 2-3 strong, movable spiniform hamate setae along posterior margin. Ischium 0.2 X length of merus. Epipod present.

Fourth pereopod reaching tip of 2nd segment to tip of 3rd segment of antennular peduncle, morphologically similar to 3rd pereopod.

Fifth pereopod reaching tip of 2nd segment to tip of 3rd segment of antennular peduncle. Dactylus unguiculate, compressed, length c. 3.8 X width, ending in claw-like apical hamate seta, bearing comb-like row of 55-65 hamate setae gradually increasing in length distally on posterior margin. Propodus length 8-10 X width, 3.6 X dactylus length, bearing two rows of 15-20 short hamate setae on posterior margin. Carpus length 0.5-0.6 X propodus length, bearing 2-7 short hamate setae, distal projection well-developed. Merus distinctly shorter (0.6-0.8 X) but broader (1.8 X) than propodus, bearing 2-4 large spiniform hamate setae. Ischium c. 0.4 X length of merus, with simple setae. Epipod absent.

Abdomen (1a) well developed, rotund, glabrous, c. 2.8 X CL; sixth abdominal segment elongate, c. 0.6 X CL, length-depth ratio c. 1.7; protopod of uropod (Figs. 3c, 2e) acute, aspinose; telson (Fig. 3b) narrow, length c. 0.7 X CL, dorsal spination (3-5 pairs) confined to posterior half of telson; posterior telsonic margin rounded, 3-4 pairs of spine-like setae, decreasing in size interiorly, median spine absent; diaeresis on telsonic exopod 10-16.

First ♂ pleopodal endopod with well developed appendix interna arising sub-distally. Appendix interna of 2nd ♂ pleopodal endopod reaching beyond middle of appendix masculina, with many retinaculae distally. Appendix masculina subcylindrical, long hamate setae distally and on inner lateral margin.

Live colour, translucent brown.

**ETYMOLOGY.** The specific epithet is chosen to highlight the fact that this new species can be confused with *Caridina zebra*.

**REMARKS.** *Caridina confusa* sp. nov. possesses a longer rostrum and is a much more slender and elongate animal than *C. zebra*. It is found primarily in open grassland streams, flowing through pastoral land of the upper Barron (Gwynne Creek) and the upper North Johnstone (Ithaca and Thiaki Creeks) catchments. Smaller numbers are found, together with *C. zebra*, in the small, remnant rainforest areas of these streams. Despite extensive sampling, *C. confusa* sp. nov. has not been found anywhere else.

### *Caridina spinula* sp. nov.

**MATERIAL EXAMINED.** HOLOTYPE. QMW-21913 adult ♀, 4.6mm CL, 1.2mm RL, 17.6mm SL, east-flowing first order tributary of Leo Creek, near crossing of Leo Creek Mine Road (13°44.6'S, 143°21.5'E), Nesbit River catchment, McIlwraith Range, Cape York, alt. c. 450m, 12.7.95, J. Marshall, N. Phillips. ALLOTYPE. QMW21914 adult ♂, 3.2mm CL, 0.8mm RL, 12.4mm SL, same locality data as holotype. PARATYPES. QMW21915 ♂♂, 7 ♀♀ (2 ovigerous), same data as holotype; QMW21922, west-flowing headwaters of Peach Creek (143°20'E, 13°44'S), Archer River catchment, McIlwraith Range, Cape York Peninsula, alt. c. 500m, 15.11.94, K. McDonald, 7 ♂♂ (3.8-4.6mm CL), 34 ♀♀ (1 ovig.) (2.6-5.4mm CL, ovig. ♀ 4.9mm).

**DIAGNOSIS.** Body rotund, rostrum short (RL < 0.4CL), dorsoventrally compressed but slightly elevated towards dorsal carina, may have a tooth on the ventral margin, reaching to tip of basal antennular segment; pterygostomian angle broadly angular to acute and spiniform; dorsal telsonic spines confined to posterior half of telson, posterior median spine may be present; eggs large (length > 1.32mm).

**DESCRIPTION.** Body (Fig. 1c) small, subcylindrical; ♂♂ in collection up to 2.7mm CL, ♀♀ up to 5.4mm CL.

Cephalothorax (Figs. 1c; 2g, h; 4g, h) round, glabrous, breadth c. 0.8 CL, depth 0.6-0.8 CL, rostrum short 0.20-0.33 CL, length 5-10 X height, curving downward, may be elevated medially, reaching tip of basal segment of antennular peduncle, may be setose dorsodistally, dorsoventrally compressed, a rostral tooth may be present on the ventral margin. Antennal spine short, placed on orbital angle; pterygostomian angle broadly angular (in Peach Creek specimens) or acute, spiniform (in Leo Creek specimens). Eyes large, c. 0.2 CL, corneal diameter c. equal eye-stalk length, retinal pigmentation present. Antennular peduncle shorter than scaphocerite, 0.6-0.7 CL; stylocerite length 0.7 X proximal

antennular segment length; anterolateral angle of proximal antennular segment acute, reaching to about 0.15 X intermediate segment length; intermediate segment 0.7 X proximal segment length, about 1.7 X distal segment length; all segments with submarginal plumose setae; distal segment fringed laterally and apically with plumose setae. Antennal peduncle 0.5-0.6 X scaphocerite length; scaphocerite slightly longer than antennular peduncle, 0.6-0.7 CL, outer margin straight to slightly concave, asetose, ending in strong subapical spine, length 2.9-3.0 X width, distal lamella and inner margin with plumose setae. Branchial formula typical for genus.

Mandibles dimorphic, without palp; right mandible with 5-6 strong, sharp incisor teeth laterally; medially two groups of setae, one group with bent hamate setae, other group with finer straight plumose setae; molar process ridged; left mandible with 5-6 strong teeth; medially three groups of setae, molar process ridged.

Maxillula with simple palp, slightly expanded distally, with long plumose setae distally, few simple setae proximally; lower lacinia with broadly rounded margin, bearing several rows of plumose and simple setae; upper lacinia broadly elongate, inner edge straight, with several rows of strong spiniform, hamate, denticulate and plumose setae, outer and lower inner margins with plumose setae.

Maxilla with slender tapering palp, shorter than upper endite cleft, setose; margin and submargin of upper and middle endite with simple, hamate, plumose and denticulate setae; lower endite with hamate setae; scaphognathite with regular row of long plumose setae on distal margin, with shorter hamate ones continuing down proximal triangular process which has c. 11 long simple setae, some with prominent dilation at base.

First maxilliped with broadly triangular lamellar palp, ending in pointed tip, margins with plumose setae; ultimate and penultimate segments of endites indistinctly divided; inner margin of ultimate segment with long denticulate setae, long rows of plumose, simple and hamate setae submarginally, transverse rows of plumose setae proximally; exopod flagellum distinct, well-developed, with submarginal and marginal plumose setae; caridean lobe narrow, with marginal and submarginal plumose setae.

Second maxilliped with dactylar and propodal segments of endopod fused; inner margins of all three proximal segments with long simple hamate and plumose setae; exopod long, narrow with

TABLE 1. Morphometric ratios (range) of pereopods of *Caridina zebra* Short, 1993, *C. confusa* sp. nov. and *C. spinula* sp. nov. D, dactylus; P, propodus; C, carpus; M, merus; L, length; W, width. 1, 2, 3 and 5 refer to the corresponding pereopods.

Attribute	<i>C. zebra</i>	<i>C. confusa</i>	<i>C. spinula</i>
D1L/D1W	3.0-3.4	2.4-3.1	2.0-3.4
P1L/P1W	2.0-2.5	1.7-2.2	2.0-2.7
C1L/C1W	1.0-2.2	1.3-1.6	1.9-2.5
M1L/M1W	2.8-4.2	2.0-2.3	2.6-4.0
D2L/P2L	0.5-0.8	0.2-0.5	0.4-3.6
C1L/P1L	0.7-0.9	0.6-0.8	0.7-1.0
M1L/P1L	0.9-1.0	0.6-0.7	0.3-0.9
D2L/D2W	4.6-4.8	4.9-5.1	3.2-4.2
P2L/P2W	2.7-3.3	2.4-2.6	2.4-2.9
C2L/C2W	3.5-6.0	3.5-4.8	3.4-6.1
M2L/M2W	5.1-5.3	4.6-4.8	4.8-5.4
D3L/P3L	0.6-0.8	0.6-0.7	0.5-0.7
C3L/P3L	0.9-1.4	1.0-1.3	1.4-1.6
M3L/P3L	1.1-1.3	1.0-1.1	1.2-1.3
P3L/P3W	7.0-10.0	8.0-11.0	10.5-13.0
C3L/C3W	4.6-4.8	4.9-5.1	4.9-5.8
M3L/M3W	4.8-5.0	5.0-5.2	5.1-6.4
C5L/P5L	0.6-0.9	0.8-1.1	0.6-0.8
M3L/P3L	1.1-1.3	1.1-1.4	1.1-1.3
P5L/P5W	11.5-14.5	8.0-11.0	12.2-16.4
C5L/C5W	4.2-5.7	4.1-4.6	3.9-5.8
M5L/M5W	5.7-7.5	5.6-6.0	6.4-6.9
C5L/P5L	0.4-0.6	0.5-0.6	0.4-0.6
M5L/P5L	0.8-0.9	0.6-0.8	0.8-0.9

marginal long plumose setae distally and shorter ones proximally.

Third maxilliped reaching beyond tip of antennular peduncle; endopod three-segmented, basal segment length c. 6.5 X width; penultimate segment length c. 8 X width, c. 0.9 X basal segment length, with transverse rows of spiniform hamate setae; distal segment c. 0.9 X as long as penultimate segment, ending in large claw-like apical hamate seta surrounded by simple and plumose ones, behind which there are 7-9 hamate setae on distal third of posterior margin, clump of serrate and pappose setae proximally; exopod reaching about 0.5 of 2nd endopod segment, distal margin with long plumose setae.

First pereopod (Fig. 4i) reaching tip of basal antennular segment; chela length 1.9-2.2 X width, movable finger 1.1 X as long as palm, length 2.0-3.4 X width; finger tips rounded, without hooks, setal brushes well-developed. Carpus attached to chela ventrally, excavated distodorsally, length 1.6-2.5 X width, 0.7-1.0 X chela length, 1.0 X merus length. Merus compressed,

TABLE 2. Distinguishing characteristics of *Caridina zebra* Short, 1993, *C. confusa* sp. nov. and *C. spinula* sp. nov. CL, post-orbital carapace length.

	<i>C. zebra</i>	<i>C. confusa</i>	<i>C. spinula</i>
Distribution	mainly in rainforest-covered streams of the upper Tully, Herbert, Johnstone and Barron catchments	open grassland reaches of streams of the upper Johnstone and Barron catchments	rainforest-covered streams of Nisbet and Archer catchments in the Mullwaith Range, Cape York
Rostrum	to tip of 2nd segment of antennular peduncle, length 0.21-0.50 CL	to beyond tip of 2nd segment of antennular peduncle, length 0.43-0.76 CL	to tip of 1st segment of antennular peduncle, length 0.20-0.33 CL
Antennular peduncle length	$0.58 \pm 0.01$ CL	$0.69 \pm 0.011$ CL	$0.58 \pm 0.01$ CL
Antennal peduncle length	$0.4 \pm 0.01$ CL	$0.51 \pm 0.01$ CL	$0.44 \pm 0.01$ CL
Stylocente	to tip of 1st antennular peduncle segment, length $0.30 \pm 0.04$ CL	not to tip of 1st antennular peduncle segment, length $0.45 \pm 0.05$ CL	not to tip of 1st antennular peduncle segment, length $0.32 \pm 0.01$ CL
Scaphocerite length	$0.61 \pm 0.02$ CL	$0.94 \pm 0.03$ CL	$0.62 \pm 0.02$ CL
Pterygostomian angle	bluntly angular	bluntly angular	acutely angular to acute, spiniform
Length of 6th abdominal segment	$0.48 \pm 0.01$ CL	$0.57 \pm 0.01$ CL	$0.50 \pm 0.11$ CL
Length-depth ratio of 6th abdom. segment	$1.26 \pm 0.07$	$1.68 \pm 0.03$	$1.65 \pm 0.08$
Propod of uropod	elongate, spinose	short, acute	elongate, spinose
Telson	short, broad, $0.53 \pm 0.02$ CL, anterior telsonic width $0.44 \pm 0.01$ telsonic length, posterior telsonic width $0.19 \pm 0.01$ telsonic length	elongate, narrow, $0.75 \pm 0.04$ CL, anterior telsonic width $0.39 \pm 0.01$ telsonic length, posterior telsonic width $1.5 \pm 0.01$ telsonic length	short, broad, $0.54 \pm 0.05$ CL, anterior telsonic width $0.41 \pm 0.01$ telsonic length, posterior telsonic width $0.20 \pm 0.01$ telsonic length
Dorsal telsonic spination	to posterior two thirds of telson	confined to posterior half of telson	to posterior two thirds of telson
Telsonic margin	median spine may be present	median spine absent	median spine may be present
Diaeresis	16-21	16-18	16-22
Unlev. egg (mm)	$0.63-0.81 \times 1.02-1.21$	$0.63-0.85 \times 0.98-1.36$	$0.80-0.85 \times 1.30-1.44$
Dev. egg size (mm)	$0.70-0.80 \times 1.22-1.32$	$0.73-0.88 \times 1.22-1.44$	not available
Number eggs/female	38-57, mean 45	28-74, mean 51.5	17-18, mean 17.5

0.6 X as wide as carpus. Ischium length 0.41 X merus length. Epipod present.

Second pereopod (Fig. 4j) reaching tip of 2nd segment of antennular peduncle, more slender and longer than 1st pereopod. Chela length 2.4-2.9 X width; movable finger length 3.2-4.5 X width, 1.6 X as long as palm; finger tips without hooks, setal brushes well-developed. Carpus subconical, length 5.8-6.1 X width, 1.4-2.0 X chela length, 1.1 X merus length. Ischium length 0.48 X merus length. Epipod present.

Third pereopod (Fig. 4k, l) over-reaching antennular peduncle tip by about 0.33 distal propodus. Dactylus sexually dimorphic in adults, length c. 2.6 X width, c. 0.25 X propodus length, ending in prominent claw-like hamate seta sur-

rounded by simple setae, behind which posterior margin bears 4-5 shorter spiniform hamate setae, these being more robust and upright in adult ♂♂. Propodus length 10.5-13.0 X width, posterior margin and lateral surface bearing rows of small spiniform hamate setae. Carpus length 0.6-0.8 X propodus length, distal projection feebly developed, posterior and lateral surfaces with 1 large and up to 5 small hamate setae, more spiniform setation in adult ♂♂. Merus 1.6-1.9 X length of carpus, with 2-4 strong, movable spiniform hamate setae along posterior margin. Ischium 0.3 X length of merus. Epipod present.

Fourth pereopod reaching tip of 2nd segment to tip of 3rd segment of antennular peduncle, morphologically similar to 3rd pereopod.

Fifth pereopod (Fig. 4m, n) reaching tip of 2nd segment to tip of 3rd segment of antennular peduncle. Dactylus unguiculate, compressed, length c. 4.0 X width, ending in claw-like apical hamate seta, bearing comb-like row of 45-55 hamate setae gradually increasing in length distally on posterior margin. Propodus length 12-15 X width, 3.3 X dactylus length, bearing rows of 10-15 short hamate setae on posterior margin. Carpus length 0.4-0.6 X propodus length, bearing 2-7 short hamate setae, distal projection well-developed.

Merus shorter (0.8-0.9 X) but broader (1.5 X) than propodus, bearing 2-4 large spiniform hamate setae. Ischium c. 0.3 X length of merus, with simple setae. Epipod absent.

Abdomen (1c) well-developed, round, glabrous, c. 3 X CL; 6th abdominal segment elongate, c. 0.5 X CL, length-depth ratio c. 1.8; propod of uropod acute, aspinose; telson (Fig. 4o) broad, length c. 0.5 X CL, dorsal spination (3-5 pairs) confined to posterior 0.66 of telson; posterior telsonic margin rounded, 4-5 pairs of spine-like setae, decreasing in size anteriorly, median spine may be present; diaeresis on telsonic exopod 16-22.

First ♂ pleopodal endopod (Fig. 4p) with well-developed appendix interna arising sub-distally.

Appendix interna of 2nd 5 pleopodal endopod (Fig. 4q) reaching beyond middle of appendix masculina, with many retinaculae distally. Appendix masculina subcylindrical, long hamate setae distally and on inner lateral margin.

Live colour, translucent brown.

**ETYMOLOGY.** The specific name refers to the distinctive, spiniform pterygostomian angle which may be present in some specimens. No other Australian *Caridina* species exhibits this spiniform pterygostomian angle.

**REMARKS.** Although *C. spinula* sp. nov. looks very much like *C. zebra*, there are distinct morphological differences (Tables 1 and 2). The spiniform pterygostomian angle in specimens from Leo Creek is also very distinctive. This species is currently known only from the McIlwraith Range in the Cape York Peninsula and, despite extensive sampling, has not been found on the Atherton Tablelands around the Lamb-Francis-Cardwell Ranges (where *C. zebra* and *C. confusa* sp. nov. are found). The only other likely area of its occurrence between the Atherton Tableland and the McIlwraith Range that we have not sampled is the Cape Tribulation/Daintree area. However, none were found here during other sampling trips (J. Short and B. Herbert, pers. comm.). The Leo Creek tributary from where *Caridina spinula* sp. nov. was collected consists of a series of riffles and pools no more than 3m long, 1m wide and 0.3m deep, flowing over a substrate of bedrock with some sand and gravel. Discharge at time of sampling was approximately  $1 \text{ L s}^{-1}$ . Vegetation in the area is tropical mesophyll rainforest with a closed canopy at only 6-8m and some emergent vegetation. The low canopy suggests that this area may have recently been disturbed (David Hanger, pers. comm.). Density of the shrimp was low ( $1\text{--}2 \text{ m}^{-2}$ ). Other animals recorded from the collection site include the prawn *Macrobrachium tolmerum* (Decapoda: Palaemonidae) and the frogs *Litoria genimaculata*, *L. longirostris* (Anura: Hylidae), *Sphenophryne gracilipes* (Anura: Microhylidae) and *Rana daemeli* (Anura: Ranidae).

## DISCUSSION

The *Caridina typus* species-group, characterised by its short, dorsally unarmed rostrum, can be identified using the key of Choy and Horwitz (1995) (to couplet 6, p. 52). The four species can then be identified using the following key.

1. Rostrum long, extending beyond tip of second segment of antennular peduncle, 0.4-0.8 times carapace length; stylocerite long, 0.4-0.5 times carapace length; sixth abdominal segment long, 0.55-0.59 times carapace length

..... *Caridina confusa* sp. nov.

Rostrum short, not reaching tip of second segment of antennular peduncle, 0.2-0.5 times carapace length; stylocerite and sixth abdominal segment short, <0.4 and <0.5 times carapace length respectively

2. Rostrum somewhat laterally flattened, with 1-5 teeth on ventral margin; posterior telson margin angular, median plumose setae on posterior telson margin with sclerotinous plug; eggs small, <0.6mm long ..... *C. typus*

Rostrum somewhat dorsoventrally flattened, ventral teeth usually absent although one may be present; posterior telson margin rounded, median plumose setae without sclerotinous plug; eggs large, >0.8mm long

3. Rostrum short, not extending beyond tip of first segment of antennular peduncle; length to depth ratio of sixth abdominal segment >1.4, number of eggs carried by female <25 ..... *C. spinula* sp. nov.

Rostrum relatively long, usually extending beyond tip of first segment of antennular peduncle, length to depth ratio of sixth abdominal segment <1.4, number of eggs carried by female >30 ..... *C. zebra*

*Caridina zebra* Short, 1993, *C. confusa* sp. nov. and *C. spinula* sp. nov. may also be separated on the basis of distinguishing characters given in Tables 1 and 2. It is emphasised that individual characters may be highly variable and so a combination of characters should be used to confirm the identity of keyed out specimens. The relationship between carapace length, rostrum, and the sixth abdominal segment lengths are linear for all three species (Fig. 5). The slopes and intercepts of the regression lines are significantly different for *C. confusa* when compared to the other two species ( $P > 0.05$ ). All three species tend to be allopatric. It is only in and near the short rainforest reaches of Gwynne and Thiaki Creeks that *C. zebra* and *C. confusa* are sympatric. Although *C. zebra* has been collected from some open, para grass infested and anthropogenically disturbed reaches of streams (e.g., Raspberry, Ithaca and Prior's Creeks) it does not appear to be very tolerant of these conditions. It seems to prefer the rainforest reaches of stream. *C. zebra* is a rotund animal, more commonly found on sandy, silty and/or leaf litter beds of riparian-covered rainforest streams and is particularly abundant in the more elevated, cooler areas (c. 800-950m), where fish predators and crustacean competitors are ab-

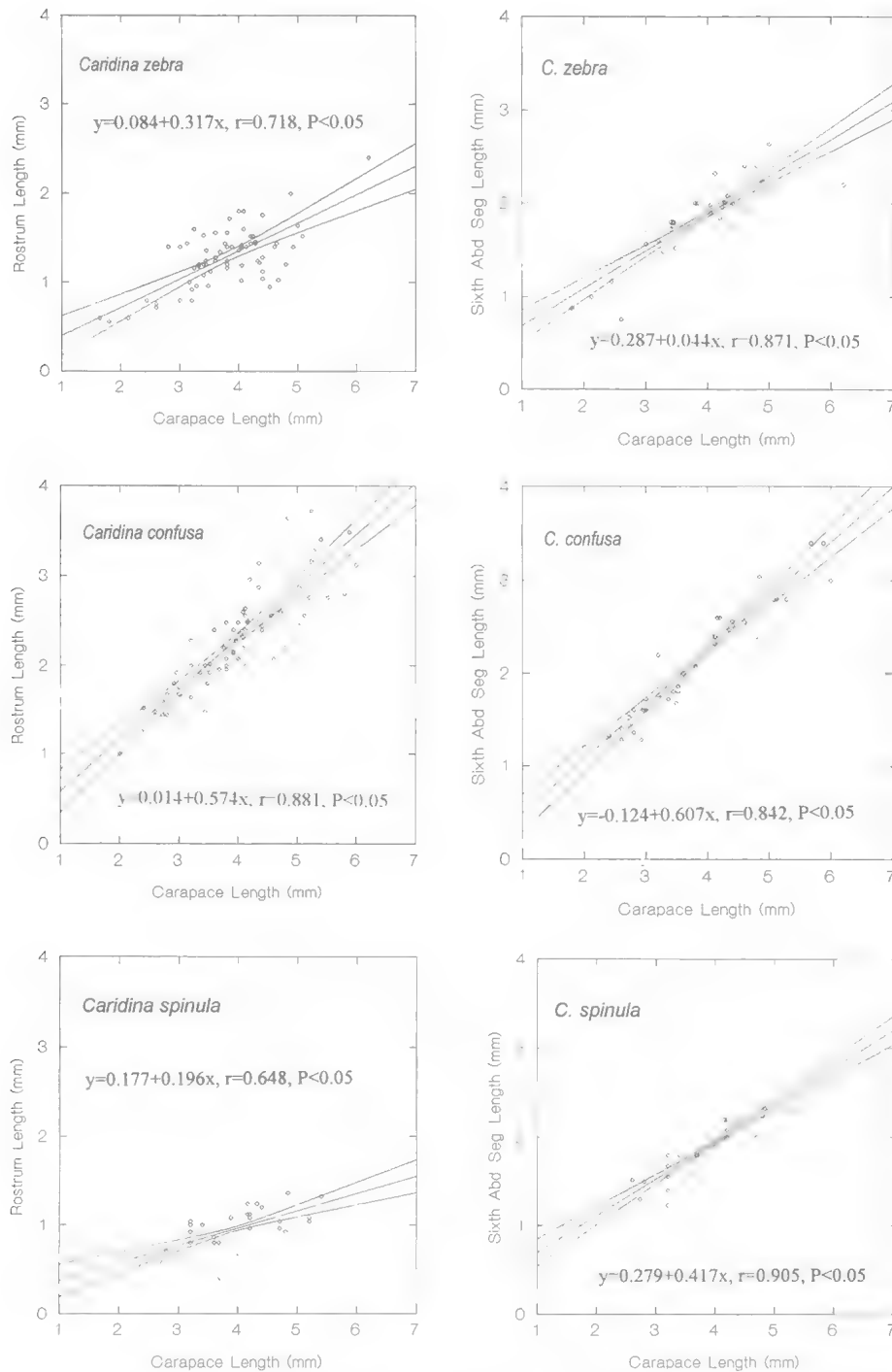


FIG. 5. Correlation between carapace length, rostrum length and sixth abdominal segment length of *Caridina zebra*, *C. confusa* sp. nov. and *C. spinula* sp. nov. All regressions are significant ( $P < 0.05$ ). The slopes and intercepts of the regression lines of the appropriate variables between *C. confusa* and *C. zebra* and between *C. confusa* and *C. spinula* are significantly different (ANOCOVA,  $P > 0.05$ ).



sent. *C. confusa* sp. nov. is a more elongate, slender animal more commonly found amongst the bank vegetation (particularly para grass) of streams flowing through open grassland areas of the Atherton Tableland.

It is likely that both the species were present in these previously rainforested areas. The modified environment may be favouring *C. confusa*, hence its predominance in these areas.

#### ACKNOWLEDGEMENTS

Stuart Bunn, Chris Marshall and David Hurwood of Griffith University, Brett Herbert of the Department of Primary Industries, Walkamin and Mark Hopper of the Department of Natural Resources, Mareeba assisted in collecting the samples. Peter Davie allowed access to the Queensland Museum collection and John Short assisted in many ways, including helpful discussion. Funding from the Co-operative Research Centre for Tropical Rainforest Ecology and Management and the Wet Tropics Management Authority (through Griffith University), the Monitoring River Health Initiative Program and the Department of Natural Resources made possible the expeditions to collect samples. Stuart Bunn, Jane Hughes and John Short provided constructive criticism of the draft manuscript.

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# GASTROPODS FROM THE BURDEKIN FORMATION, MIDDLE DEVONIAN, NORTH QUEENSLAND

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Cook, Alex G. 1997 06 30: Gastropods from the Burdekin Formation, Middle Devonian, north Queensland. *Memoirs of the Queensland Museum* 42(1): 37-49, Brisbane, ISSN 0079-8835.

Twenty one taxa of gastropods are described from the Middle Devonian Burdekin Formation, north Queensland. New amongst these are *Burdekinostoma burdekinensis* gen. et. sp. nov., *Euryzone burdekinensis* sp. nov., *Anomphalus pajelli* sp. nov., *Didymalgia bartholomai* gen. et sp. nov., *Murchisonia (Murchisonia) jackelli* sp. nov., *Palaeozygopleura mackenryi* sp. nov., and *Trinema heideckeri* gen. et sp. nov. The fauna contains typical Old World Realm genera but is specifically strongly endemic. □ *Gastropods, Devonian, Queensland, Burdekin Formation.*

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Burdekin Formation is a shallow marine carbonate sequence exposed within the Burdekin Subprovince (Wyatt & Jell, 1967; Henderson, 1980; ). The formation consists of, inter alia, a reefal and biostromal complex, with associated lagoonal, inter-reef and offshore facies (Cook, 1995). It contains diverse fossil assemblages which include rugose corals (Zhen 1991, 1994), tabulate corals, stromatoporoids (Cook, 1994), sponges, molluscs (Cook, 1993a) and conodonts (Talent & Mawson, 1994). Large, thick-shelled gastropods from the underlying and interdigitating, siliciclastic-dominated, Big Bend Arkose and basal units of the Burdekin Formation are *Burdekinia burdekinensis* (Etheridge, 1917), *Amphelissa carinatum* (Heidecker, 1959), *Labrocuspis nodosa* Heidecker, 1959, and *Fletcheriella septata* Cook, 1993b.

This paper is concerned with a diverse gastropod faunule from a stratigraphically higher unit in the Burdekin Formation in coralline packstones interpreted to represent shallow-water coralline thickets seaward of a biohermal structure (Cook, 1995). The fauna has been silicified and was recovered by bulk dissolution in acetic acid. Both large and small gastropods were retrieved, in addition to corals, brachiopods and bivalves. All material comes from QML1094, near Little Rocks, 27km NW of Charters Towers.

## SYSTEMATIC PALAEONTOLOGY

Phylum MOLLUSCA  
Class GASTROPODA  
Order ARCHAEOGASTROPODA  
Superfamily BELLEROPHONTOIDEA  
Family BELLEROPHONTIDAE McCoy, 1851  
Subfamily TROPIDODISCINAE Knight, 1956

*Tropidodiscus* Meek & Worthen, 1866  
*Tropidodiscus* sp.  
(Fig. 1A-C)

MATERIAL EXAMINED QMF35513, QMF35514.

DESCRIPTION. Shell minute, approximately 2.5mm in diameter, 0.8mm wide; involute with moderately wide umbilicus. Whorl profile sharply angular, without obvious crest. Relics of fine, numerous growth lines present.

*Bellerophon* de Montfort, 1810

*Bellerophon (Bellerophon)* de Montfort, 1810

*Bellerophon (Bellerophon)* sp. A  
(Fig. 1D,E)

MATERIAL EXAMINED. QMF34916, QMF34962.

DESCRIPTION. Small to medium-sized, spherical, involute, 5.5mm wide; narrow deep umbilicus. Whorl profile evenly rounded; margin bearing weak crest. Aperture unknown. Ornament consists of many fine growth lines.

REMARKS. The few specimens possess similar characteristics to the type, *B.(B.) vasulites* de Montfort, 1810 from the Middle Devonian of

Germany as figured by Knight (1941). The numerous growth lines and overall form are similar, but the Burdekin form is much smaller (Knight, 1941: pl. 11) and the selenizone-bearing crest is weaker, possibly due to imperfect silicification.

**Bellerophon (Bellerophon) sp. B**  
(Fig. 1F,G)

MATERIAL EXAMINED. QMF34908.

DESCRIPTION. Spherical, medium-sized, approximately 10mm in diameter, 9mm high; involute with deep, wide umbilicus. Whorl profile wide and rounded with weak crest; slight flattening of inner whorl surface adjacent to penultimate whorl, extending approximately one third across the inner whorl profile.

REMARKS. The specimen is larger and has a wider whorl profile than *Bellerophon* (*Bellerophon*) sp. A, which is a result of the flattened area on the whorl profile abutting the penultimate whorl.

Superfamily EUOMPHALOIDEA  
de Koninck, 1881  
Family EUOMPHALIDAE de Koninck, 1881

**Straparollus** de Montfort, 1810  
**Straparollus (Euomphalus)** Sowerby 1814

**Straparollus (Euomphalus) sp.**  
(Fig. 1Q)

MATERIAL EXAMINED. QMF34965.

DESCRIPTION. Medium-sized, planispiral, 21.4mm wide, 8.2mm high. Suture in a channel. Whorl profile square with prominent angulation above and below gently convex midwhorl surface. Weak spiral line adumbilically to the upper angulation which may mark the position of the sinus. Aperture rounded, but quadrate. Base flattened.

**Straparollus (Serpulospira)** Cossman, 1916  
**Straparollus (Serpulospira) sp.**  
(Fig. 1R)

MATERIAL EXAMINED. QMF34966.

DESCRIPTION. Shell planispiral, disjunct, 13.6mm wide, 4.6mm high. Whorl profile rounded, aperture rounded. No growth lines preserved.

Suborder PLEUROTOMARIINA  
Cox & Knight, 1960  
Superfamily PLEUROTOMARIOIDEA  
Swainson, 1840

Family RAPHIOSTOMATIDAE Koken, 1986  
Subfamily OPHILETINAE Knight, 1956

**Burdekinostoma** gen. nov.

TYPE SPECIES. *Burdekinostoma burdekinensis* sp. nov.

ETYMOLOGY. For the Burdekin River, and alluding to the Raphiostomatidae.

DIAGNOSIS. Minute, low-spired to lenticular, gradate shell, widely phaneromphalous, having a commonly channeled suture and prominent, gently inclined, flattened area on the upper whorl surface bordered by 2 strong cords, inferred to contain the selenizone and also commonly containing weak threads; midwhorl profile generally subrounded but stepped with several cords.

REMARKS. Placement of this striking if minute genus is difficult, as it superficially resembles members of the Ophiletinae, Raphiosomatinae and Euomphalidae. Placement depends on the interpretation of the inclined surface on the upper whorl face, which is inferred to contain the selenizone. In particular the raphiostomine *Wisconsinella* Blodgett (1988) from the Eifelian of North America is a similar taxon to the Burdekin material, sharing the gradate shell form, but lacking the additional cords and the channeled suture. Placement within the Raphiostominae is restricted by the widely phaneromphalus nature of this snail. Alternatively the channeled suture may be interpreted as containing a sinus, which would ally the genus to the Euomphalidae, of which *Poleumita* Clarke & Ruedemann and *Cenitifugus* Bronn are similar cord-bearing forms. Neither of these placements is satisfactory. Placement in the Ophiletinae best satisfies the interpretation of the selenizone, accommodates the channelled suture and the phaneromphalous condition.

**Burdekinostoma burdekinensis** sp. nov.  
(Fig. 2J-P)

MATERIAL EXAMINED. HOLOTYPE: QMF34961.  
PARATYPES: QMF35522-QMF35530.

ETYMOLOGY. From the Burdekin River.

DIAGNOSIS. As for genus.

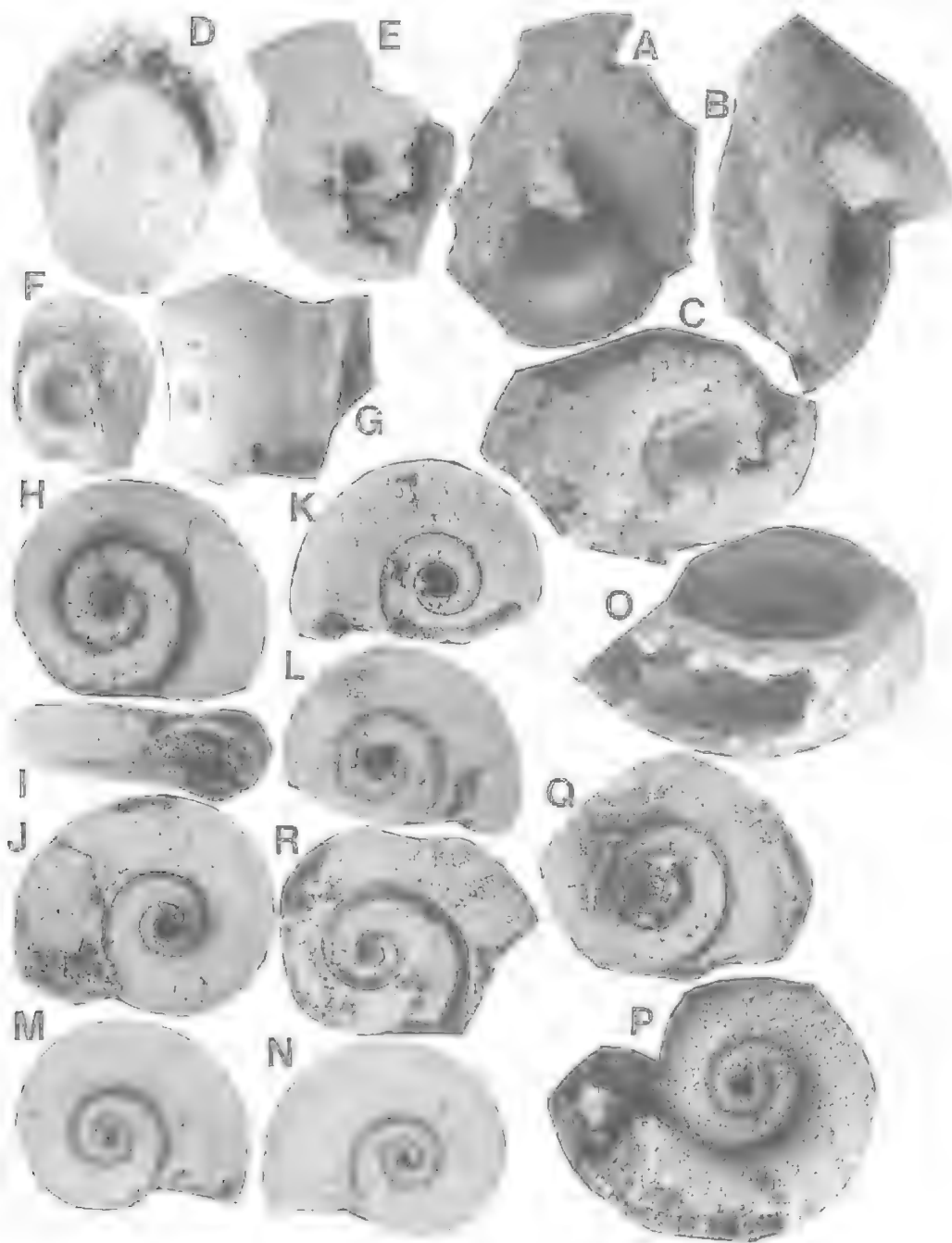


FIG. 1. A-C. *Tropidodiscus* sp. SEM images. A,B, QMF35512, side and oblique views respectively, x 16; C, QMF35513, side view, x 16. D-E. *Bellerophon* (*Bellerophon*) sp. A, QMF34916, apertural and side views respectively. F, G. *Bellerophon* (*Bellerophon*) sp. B, QMF34908, side and broken apertural views respectively. H-P. *Euryzone burdekinensis* sp. nov. H-J, Holotype QMF34917, apical apertural and basal views respectively, x 4.4; K,L, Paratype QMF 34969, basal and apical views, x 3.2; M,N, Paratype QMF34964 apical and basal views x 6.3; O, Paratype, QMF35536 oblique side view, x 22.5. SEM image: P, Paratype QMF35536 apical view x 22.5, SEM image. Q, *Straparollus* (*Euomphalus*) sp. QMF34965 apical view, x 1.8. R, *Straparollus* (*Serpulospira*) sp. QMF34966, apical view x 2.3.

**DESCRIPTION.** Shell small to minute, less than 1.5 mm wide and 1.5 mm high, very low-spined, somewhat gradate, widely phaneromphalous, with deep umbilicus. Whorl profile series of angular surfaces but giving an overall rounded profile. Suture with adjacent, wide channel. Upper whorl face bears numerous spiral threads, of at least 2 orders of intensity. Three prominent threads on smaller specimens; bordering the sutural channel, another high on the whorl profile and another at the edge of the upper whorl face giving way to the steeper midwhorl surfaces, the last 2 inferred to contain the selenizone. At least 2 threads on the midwhorl, creating a vertical surface at the midwhorl periphery; at least 3 revolving cords on the lower whorl face. The upper whorl face bears up to 7 minor spiral threads, in addition to the major cords.

**REMARKS.** This striking taxon is easily differentiated by *Euryzone burdekinensis* sp. nov. by the numerous spiral threads and more angular whorl profile.

Family GOSSELETINIDAE Wenz, 1938  
Subfamily COELOZONINAE Knight, 1956

*Euryzone* Koken, 1896  
*Euryzone burdekinensis* sp. nov.  
(Fig. 1H-P)

**MATERIAL EXAMINED.** HOLOTYPE: QMF34917. PARATYPES: QMF34918-QMF34927, QMF34964, QMF34969.

**DIAGNOSIS.** Small to minute member of genus with sinus on upper whorl profile bounded by fine threads.

**DESCRIPTION.** Shell discoidal, minute to small, up to 11.9 mm wide, 3.6 mm high, generally smaller (Table 1). Whorls abut, with impressed suture. Base with moderately deep umbilicus. Whorl profile rounded, bearing two fine cords which border the sinus. Growth lines fine, numerous. Shell repair in evidence on holotype.

**REMARKS.** The species is characterised by its discoidal shape and the striking presence of the sinus on the upper whorl face and its bordering cords. The most similar member of the genus to the Burdekin material is *Euryzone petilitornata* Linsley 1968 from the Middle Devonian Anderson Limestone, Michigan, but its selenizone is slightly lower on the whorl profile, and it is a less planispiral than the Burdekin species. The type species *E. delphinuloides* (Schothheim) from

TABLE 1. Measurements for *Euryzone burdekinensis* sp. nov.

Specimen	Height (mm)	Width (mm)
Holotype	3.6	10.9
QMF34969	3.6	10.0
QMF34964	3.0	4.8
QMF34915	3.1	7.3
QMF34921	1.6	5.0

the Middle Devonian *Stringocephalus* Limestone, Germany, has a turbiniform shell and a wider selenizone.

Suborder TROCHINA Cox & Knight, 1960  
Superfamily ANOMPHALOIDEA Wenz, 1938  
Family ANOMPHALIDAE Wenz, 1938

*Anomphalus* Meek & Worthen, 1867

**TYPESPECIES.** *Anomphalus rotulus* from the Middle Pennsylvanian, St Davids Limestone, Illinois, USA, by original designation.

*Anomphalus pajelli* sp. nov.  
(Fig. 2A-J)

**MATERIAL EXAMINED.** HOLOTYPE: QMF34850. PARATYPES: QMF34851-QMF34858.

**ETYMOLOGY.** For Peter A. Jell.

**DIAGNOSIS.** Smooth-shelled, medium-sized member of genus with very weak sutures and prominent thickening of inner lip which creates a hemiophalus base.

**DESCRIPTION.** Medium-sized, low-spined, rotelliform hemiophalus gastropod, up to 11.5 mm high, 13.5 mm wide (Table 2). Sutures flush, commonly difficult to detect, whorls embrace high on upper whorl surface. Umbilicus narrow obscured or occluded by thickening at the inner labrum, otherwise base rounded. Whorl profile rounded with periphery at midwhorl. Aperture rounded. Shell thick, inner labrum particularly thickened forming partial umbilical plug. Shell smooth, very faint growth lines on the base of QMF34851. There is some variation in the taxon with respect to where the whorls embrace. On QMF34851 the whorls embrace further down the whorl face, producing a slightly more naticiform shell shape. Despite silica replacement the smooth shell has an almost polished appearance on some specimens.

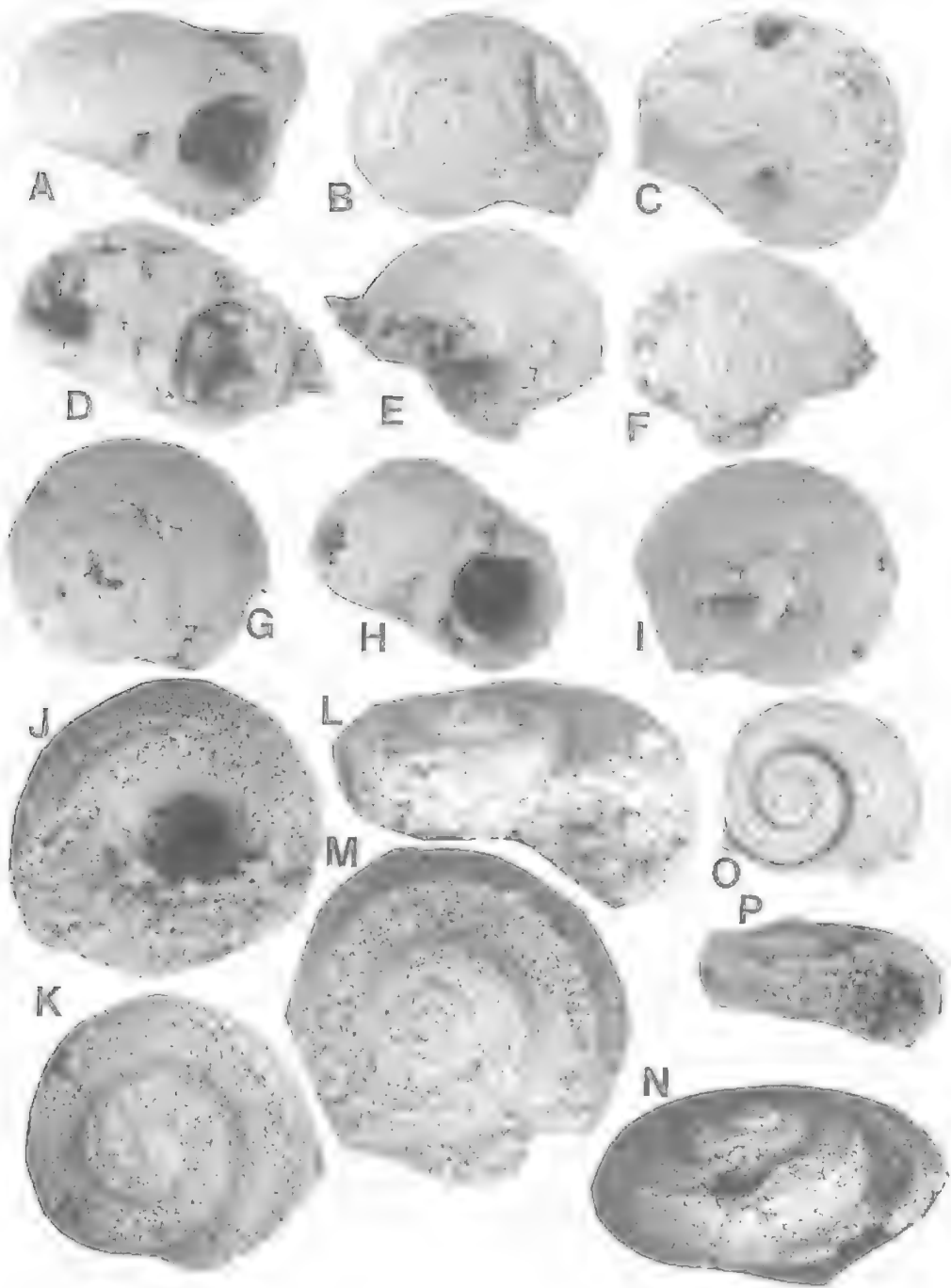


FIG. 2. A-I, *Anomphalus pajelli* sp. nov. A-C, Holotype QMF34850, apertural, apical and basal views,  $\times 9$ . D-F, Paratype QMF34852, apertural, basal and apical views,  $\times 2.2$ . G-I, Paratype QMF34851 apical, apertural and basal views,  $\times 2.5$ . J-P, *Burdekinostoma burdekinensis* gen. et sp. nov. J,K, Paratype QMF35523, basal and apical views, SEM images,  $\times 13.5$ ; L,M, Paratype QMF35522, oblique apertural and apical views, SEM images,  $\times 15$ ; N, QMF35525 side view,  $\times 13.5$ ; O,P, Holotype QMF34961,  $\times 5.4$ , apical and side views respectively.

TABLE 2. Measurements for *Anomphalus pajelli* sp. nov.

Specimen	Height (mm)	Width (mm)
QMF34850	10.7	13.1
QMF34851	11.5	13.5
QMF34852	7.5	11.1
QMF34853	7.2	11.1

REMARKS. Both Knight (1941) and Knight et al. (1960) noted the variable umbilicus in this genus. The Burdekin material is assigned to the genus on the basis of gross shape, lack of ornament and the hemiophalus condition. The type species *A. rotulus* Meek & Worthen as figured by Knight (1941) has a slightly lower whorl profile and more prominently incised sutures. *Anomphalus umbilicoliratus* Batten (1966) from the Lower Carboniferous Hotwells Limestone, England is clearly phaneromphalous and has spiral ornament on the base. *Anomphalus helicinaeformis* (Schlotheim) from the Middle Devonian *Stringocephalus* Limestones near Gladbach, Germany has a fully developed umbilical plug (see Knight 1941: pl 63), but in overall aspect is most similar to the Burdekin species, and is closely related. Specimens illustrated by Knight (1941) show minor variation in spire height for *A. helicinaeformis* (Schlotheim). *Naticopsis margheriti* Mansuy (1912), may also be an *Anomphalus*, albeit with a slightly more naticiform shell.

Suborder NERITOPSINAE Cox & Knight, 1960  
Superfamily NERITOIDEA Rafinesque, 1815  
Family NERITOPSIDAE Gray, 1847

*Naticopsis* M'Coy, 1844

*Naticopsis* (*Naticopsis*) sp.  
(Fig. 4A)

MATERIAL EXAMINED. QMF34913.

DESCRIPTION. Very small, 4.9mm wide, 5mm high, naticiform, anomphalous; suture adpressed to slightly impressed; whorl profile rounded, with periphery well above midwhorl. Upper whorl surface flatter than lower whorl face. Final whorl dominated by strong collabral cords, increasing in intensity towards the aperture. Early whorls lack this ornament. Parietal and inner lip heavily thickened; aperture ovate. Base rounded.

REMARKS. The specimen strongly resembles *Natica nexicosta* (Phillips) of Whidborne (1892),

from the Middle Devonian at Lummaton, England, but the latter possesses strong collabral cords on early whorls. *Naticopsis* (?*Naticopsis*) sp. (Rollins, Eldridge & Spiller, 1971), from the Middle Devonian Marcellus Formation, New-York, shows a similar ornament, but the threads are fine and inclined on the whorl face. *Straparollus corrugatus* (Stauffer, 1909), which Linsley (1968) placed within ?*Isonema*, and Rollins, Eldridge & Spiller (1971) assigned to *Naticopsis* (*Naticopsis*), from the Middle Devonian of Ohio also shows strong collabral ornament, but not restricted to the mature whorls. ?*Isonema corrugatus* (Stauffer) from the Middle Devonian Anderson Limestone (Linsley, 1968) is a minutely illustrated taxon. Linsley (1968) describes the early whorls as smooth suggesting affinity to the Burdekin specimen. Positive generic identification of Linsley's taxon is impossible without viewing his material. I place *Natica nexicosta* (Phillips) of Whidborne and *Straparollus corrugatus* Stauffer both within *Naticopsis* (*Naticopsis*) alongside this distinct, if poorly preserved and unresolved, taxon from the Burdekin Formation.

Superfamily ORIOSTOMATOIDEA Wenz, 1938  
Family ORIOSTOMATIDAE Wenz, 1938

*Didymalgia* gen. nov.

TYPE SPECIES. *Didymalgia bartholomai* sp. nov.

ETYMOLOGY. For 'Didymalgia' hill, informal name of laterite profile near the Fletcherview locality.

*Didymalgia bartholomai* gen. et sp. nov.  
(Fig. 3)

MATERIAL EXAMINED. HOLOTYPE: QMF34896.  
PARATYPES: QMF34876-QMF34895, QMF34915.

ETYMOLOGY. For Alan Bartholomai.

DIAGNOSIS. Turbiniform, widely phaneromphalous shell with numerous revolving cords and strong comarginal cords forming and cancellate structure, whorl profile angular, formed by series of inclined surfaces.

DESCRIPTION. Medium-sized, turbiniform, widely phaneromphalous shell, up to 9.5mm high and 11.1mm wide (Table 3). Whorl face adorned with strong revolving cords and slightly less strong comarginal ribs, producing a cancellate shell decoration. Whorl profile series of angular surfaces with a subsutural shelf, steeply inclined upper whorl face, angular periphery,



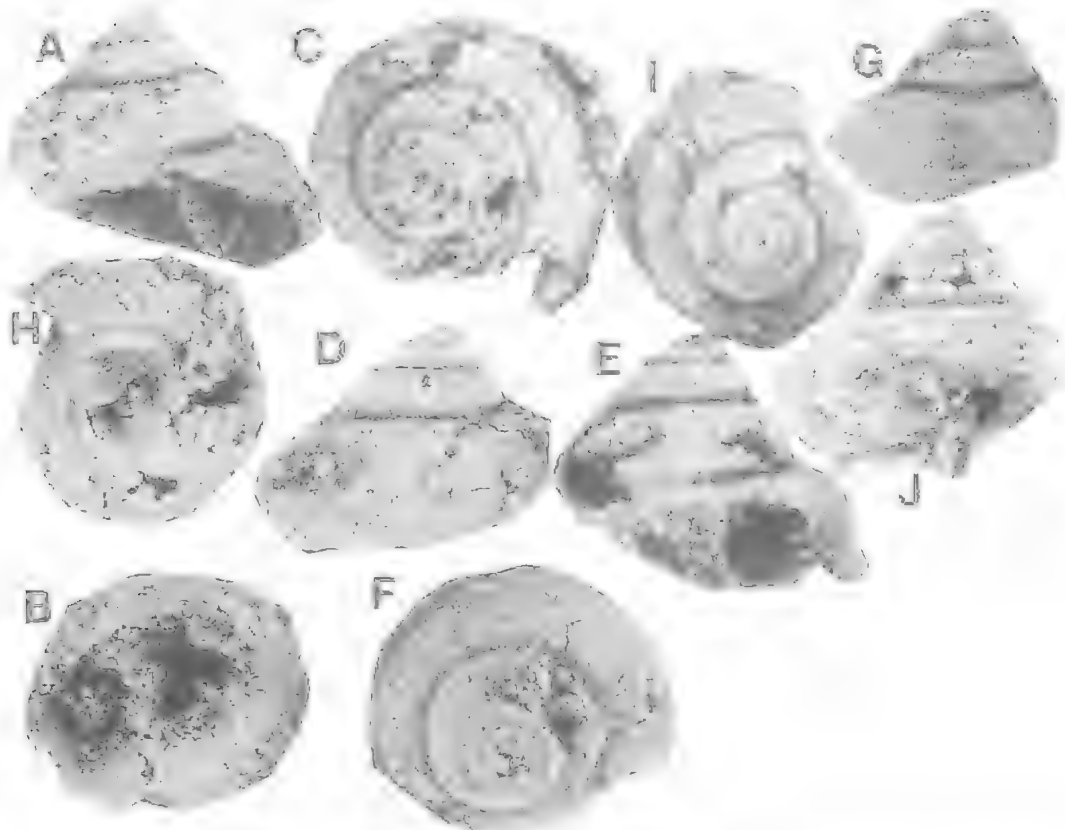


FIG. 3. *Didymalgia bartholomai* gen. et sp. nov. A-D, Holotype QMF34896, x 3 apertural, basal (x 2.8), apical and side views (x 2.8). E-G, Paratype QMF34875. E, apertural view x 5; F, apical views x 5; G, side view x 4. I-J, Paratypes QMF34876, x 3 apical and side views.

inclined lower surface leading to the phaneromphalous base, sutures embrace just below periphery which is situated slightly below mid-whorl. Slight subsutural shelf, 4 major revolving cords on the upper whorl face, a major cord at the periphery, and 7 to 8 cords on the lower whorl face and base. Two orders of cords on the lower whorl face. Aperture rounded to subrounded, slightly wider than high. Thick colabral cords are numerous almost orthocline, and are not deflected by a sinus or selenizone.

REMARKS. *Oriostoma* sp. aff *O. gerbaulti* Oehlert of Blodgett & Johnson (1992) from the Eifelian of Nevada is grossly similar to the Burdekin material but has a channeled subsutural zone. *Gyronema multinodosa* Blodgett & Johnson from the Eifelian of Nevada, which could be accommodated in *Kitikamispira*, has fewer cords and more prominent nodes on the shell surface. Placement of the genus within the Ori-

ostomatidae is problematic, in that it extends the range of the family beyond their supposed Eifelian demise (Blodgett et al. 1990), but the strong ornament, lack of selenizone on the whorl face and trochiform, phaneromphalus shell form make the placement appropriate, if controversial.

TABLE 3. Data for *Didymalgia bartholomai* gen. et sp. nov.

Specimen	Height (mm)	width (mm)
QMF34896	9.5	11.1
QMF34876	8.8	8.8
QMF34875	7.2	8.4

Suborder MURCHISONIINA Cox & Knight, 1960  
 Superfamily MURCHISONIOIDEA Koken, 1896  
 Family MURCHISONIIDAE KOKEN, 1896

*Murchisonia* d'Archaic & de Verneuil 1841

*Murchisonia* (*Murchisonia*) *jackjelli* sp. nov.  
 (Fig. 4B-H)

MATERIAL EXAMINED. HOLOTYPE: QMF34905.  
 PARATYPES: QMF34897-QMF34900, QMF34902,  
 QMF34903, QMF34929, QMF34932, QMF34933,  
 QMF34935-QMF34940, QMF34942-QMF34943,  
 QMF34946-QMF34948, QMF34952-QMF34953.

ETYMOLOGY. For J.S. Jell.

DIAGNOSIS. Medium-sized member of subgenus with a relatively wide selenizone, subrounded whorl profile and up to 5 threads on the adult lower whorl surface.

DESCRIPTION. Medium-sized to large, high-spined shell, up to 41.5mm long and 11.6mm wide at base. Suture impressed, whorls embrace at approximately lower one third of the whorl height. Whorl profile subrounded but with 2 weak peripheral cords bordering a wide selenizone. Up to 5 additional weaker spiral threads on the lower whorl face with 2 extremely faint threads on the upper surface. In juvenile specimens cords bordering the selenizone are stronger on early whorls, and the lower whorl face lacks the multiple threads of the adult whorls, instead 1 or 2 threads are more prominent. Aperture ovate with minor thickening of the inner lip.

REMARKS. Poor preservation of the material significantly impedes the study of this species. Clearly the presence of the wide midwhorl selenizone denotes the subgenus, and the numerous weak threads on adult whorls distinguish a new taxon. The width of the selenizone and the numerous threads may suggest Carboniferous *Stegocoelia*, but the selenizone is at the periphery negating that assignment. In the Middle Devonian *Murchisonia* (*Murchisonia*) underwent significant radiation into a multitude of unusual shell forms (Knight et al. 1960; Blodgett et al., 1990) and the included species described to date are numerous (e.g., Whidborne, 1892). Taxa with similar multiple threads on the whorl face are *M. (M.) vicariana* Whidborne, *M. (M.) loxonemoides* Whidborne, both from the Middle Devonian of Southern England, but the former has nodose threads and the latter a thinner, lower set selenizone.

*Murchisonia* (*Murchisonia*) sp. A.  
 (Fig. 4I-J)

MATERIAL EXAMINED. QMF34930.

DESCRIPTION. Small, 10.5mm high, 5.3mm wide, high-spined, with eight whorls present. Suture strongly impressed, whorls embrace well below midwhorl; angular whorl profile with 2 prominent spiral cords bordering a selenizone. Other decoration not preserved.

REMARKS. A selenizone on the midwhorl, bordered by 2 cords is the classic *murchisonioid* condition and the specimen is here allocated to the subgenus on this basis. The species resembles *M. (M.) fermioni* Tassell, 1982, from the Emsian of New South Wales, and also known from the Givetian in the Broken River Province, but the material is too poorly preserved to be confident of any specific assignment.

*Murchisonia* (*Murchisonia*) sp. B.  
 (Fig. 4K)

MATERIAL EXAMINED. QMF35520.

DESCRIPTION. Shell small, 6mm high, 2mm basal width, high-spined, with 7 whorls present. Sutures impressed, whorls embrace just below periphery. Whorl profile angular with 2 strong cords bordering a selenizone at the periphery, the upper cord slightly stronger. Upper whorl face gently sloped with a weak spiral cord close to the main ornament on the margin. Lower whorl profile obscured, aperture and base unknown.

REMARKS. The bordered selenizone identifies the subgenus. It is higher-spined than *Murchisonia* (*Murchisonia*) sp. A. and has a significantly different whorl profile than *Murchisonia* (*Murchisonia*) *jackjelli* sp. nov.

Superfamily CRASPEDOSTOMIDOIDEA  
 Wenz, 1938  
 Family CODONOCHEILIDAE Miller, 1889

*Mitchellia* de Koninck, 1876

?*Mitchellia* sp.  
 (Fig. 4L,M)

MATERIAL EXAMINED. QMF35515, QMF35516.

DESCRIPTION. Two fragmental specimens, neither of which have a gerontic stage or aperture preserved. Small high-spined gastropod with impressed suture; whorls embrace just below mid-

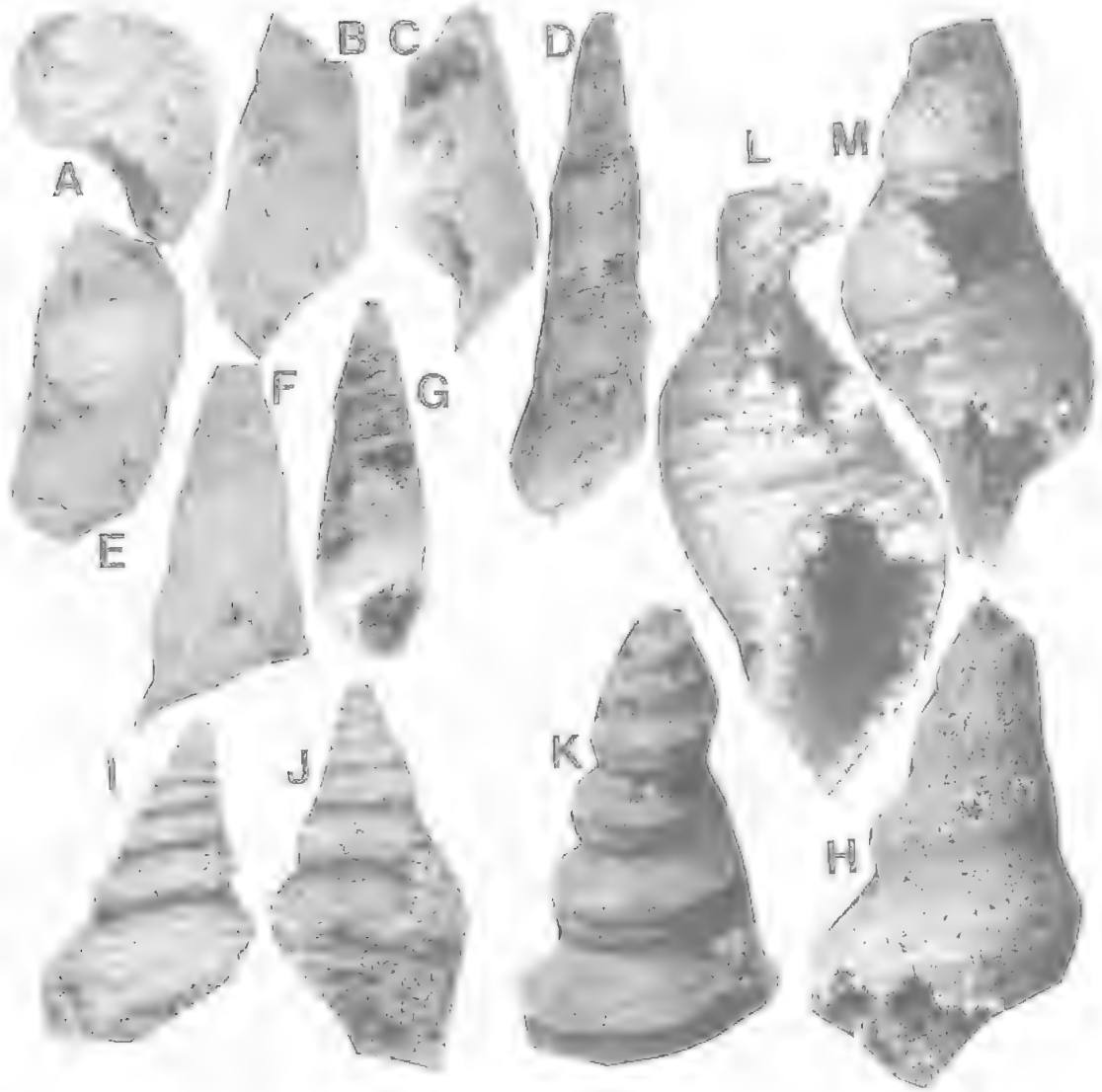


FIG. 4. A, *Naticopsis (Naticopsis)* sp. QMF34913, oblique apical view, x 5. B-H, *Murchisonia (Murchisonia) jackjelli* sp. nov. B, C, Holotype QMF34905, side views x 2.8; D, Paratype QMF34900, side view x 1.5; E, Paratype QMF34897, side view x 2; F, Paratype QMF34903, side view x 2.6; G, Paratype QMF34899 apertural view x 1.6; H, Paratype QMF35520, side view x 12. I, J, *Murchisonia (Murchisonia)* sp. A. QMF34930, x 3.5. I, side view; J, apertural view. K *Murchisonia (Murchisonia)* sp. B, side view x 10. L, M, ?*Mitchellia* sp. L, QMF35515, x 20; M, QMF35516 x 20.

whorl. Whorl profile rounded, face bearing numerous. (up to 10) spiral threads of equal intensity. Aperture not preserved, but inner whorl profile ovate with long axis vertical.

**REMARKS.** Generic assignment is impossible without more material, but the material is questionably assigned to the common eastern Austra-

lian Emsian genus on the basis of gross shell shape. It lacks the characteristic aperture needed for more definite assignment to the taxon.

Order CAENOASTROPODA Cox, 1959  
 Superfamily LOXONOMATOIDEA Koken, 1889  
 Family PALAEOZYGOPLURIDAE Horny 1955

**Palaeozygopleura** Horny, 1955

**Palaeozygopleura machenryi** sp. nov.  
 (Fig. 5A-F)

MATERIAL EXAMINED. HOLOTYPE: QMF35531.  
 PARATYPES: QMF35532-QMF35525, QMF35539.

ETYMOLOGY. For Colin McHenry.

DIAGNOSIS. Small to minute member of genus with moderately impressed suture and only slightly sigmoidal ribs.

DESCRIPTION. Shell high-spired, many whorled, up to 8 present, up to 4mm long and 1.6mm wide. Sutures impressed, whorls embrace well below midwhorl; whorl profile rounded. Periphery at midwhorl. Whorl face bears many slightly sigmoidal ribs, obvious on all adult whorls. Protoconch poorly preserved, but smooth and dextral.

REMARKS. The material is most similar to *P. joanni* Linsley from the Middle Devonian Anderson Limestone of Michigan, but in the Burdekin species the ribs are less numerous and the suture less impressed. It differs from the single specimen *Palaeozygopleura* sp. described below by the more impressed sutures and coarser ornament.

**Palaeozygopleura** sp.  
 (Fig. 5G)

MATERIAL EXAMINED. QMF35519.

DESCRIPTION. Minute, 3.6mm high, 1.5mm wide, high-spired, nearly pupiform with shallowly impressed suture, gently rounded whorl profile. Ornament consists of fine, prosocline threads on the whorl surface.

REMARKS. The single specimen has weaker sutures than *P. machenryi* sp. nov. and finer prosocline ornament.

Family TURRITELLIDAE Woodward, 1851

**Trinema** gen. nov.

TYPE SPECIES. *Trinema heideckeri* sp. nov. from the Middle Devonian Burdekin Formation, north Queensland.

ETYMOLOGY. Tri-, three, nema (Greek) thread.

DIAGNOSIS. Small to medium-sized, anomphalous, high-spired, many whorled shell; whorl profile rounded, bearing three prominent midwhorl cords. Suture impressed; a subsutural surface is bounded below by a weak thread which forms the upper limit of the deep sinus, in turn bounded below by the highest of the three midwhorl cords. Finer threads are present on the lower whorl face. Growth lines are prosocline above the sinus and opisthocline below. Whorls embrace just below the higher of the weak threads on the lower whorl face.

REMARKS. Placement in the family is indicated by the overall shell form and the position of the sinus above the midwhorl cords (see Knight et al. 1960: 1317). The taxon is differentiated by the only other Devonian turritellid (Linsley 1978), *Acanthonema* Sherzer & Grabau, 1908 by lacking the distinctive nodose cords. In the Late Carboniferous *Orthonema* Meek & Worthen, 1861 (see Knight 1934, 1941, Knight et al., 1960) there are 2 prominent midwhorl cords, widely separated below the similarly positioned sinus. In *Callispira* Nelson, 1947, the sinus is also positioned high on the whorl face, but the whorl face is less rounded and there are many more stronger cords (5-6) on the whorl face. There is a considerable gap in the taxonomic record of the Turritellidae between the appearance of *Acanthonema* in the Early Devonian (Sherzer & Grabau, 1908), their Middle Devonian record (herein) and the numerous Carboniferous records of *Orthonema* (Knight, 1934). Such a discontinuity in the record may be resolved by analysis of Late Devonian age faunas.

**Trinema heideckeri** sp. nov.  
 (Fig. 5H-K)

MATERIAL EXAMINED. HOLOTYPE: QMF34954.  
 PARATYPES: QMF34941, QMF34945, QMF34955.

DIAGNOSIS. As for genus.

DESCRIPTION. Material somewhat fragmental, Shell small- to medium-sized, anomphalous, high-spired, up to 12 whorls present. Whorl profile rounded overall, slightly more convex on lower whorl face; periphery at midwhorl. Suture impressed with subsutural face bordered below by weak spiral thread. Midwhorl face dominated by 3 strong spiral cords the middle of which is slightly weaker. Between the uppermost of the strong peripheral cords and the weak cord below

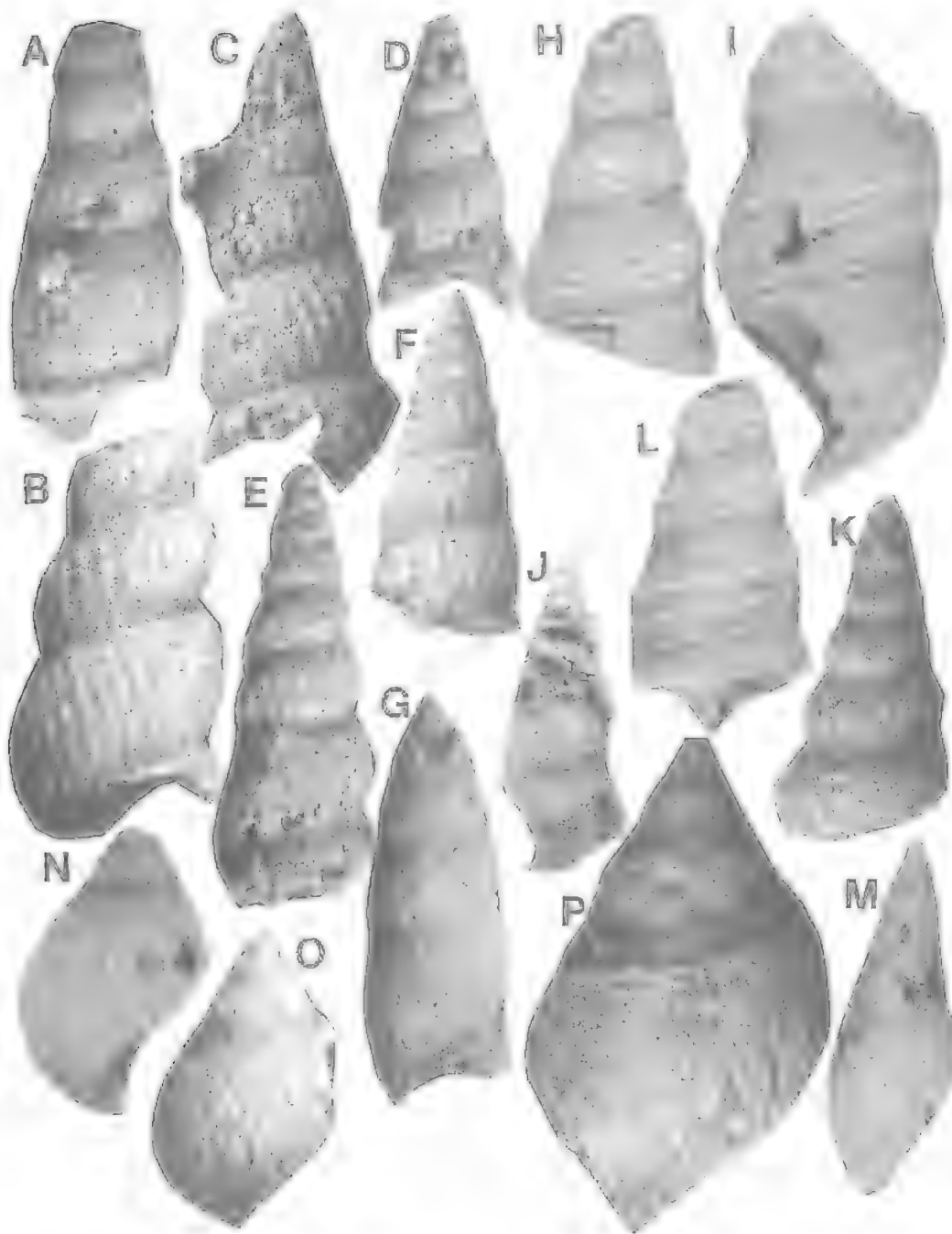


FIG. 5. A-F, *Palaeozygopleura machenryi* sp. nov., all SEM images. A, Paratype QMF35532, x 19; B, QMF35533 x 17; C, QMF35534, x 21; D, QMF35535, x 19; E, QMF35538, x 15; F, Holotype QMF35531, x 17. G, *Palaeozygopleura* sp. QMF35519, x 15. H-K, *Trinema heideckeri* gen. et sp. nov. H, Paratype QMF34941, x 4.3; I, Holotype QMF34954, side view x 5; J, Paratype QMF34955, x 2.5; K, Paratype, L, Paratype QMF34945, small specimen, x 19 SEM image. L, *Trinema* sp. QMF34931, x 4.3. M, ?*Subulites* (*Subulites*) sp. QMF34934, x 4.2. N, ?*Subulites* (*Fusispira*) sp. A, QMF34912, x 6.1. O, P, ?*Subulites* (*Fusispira*) sp. B, QMF35517, x 9, x 17 respectively.

the suture lies the trace of the deep sinus, indicated by the growth lines. Three weak spiral cords are present on the lower whorl face. Growth lines fine, numerous, prosocline above the sinus and opisthocline below. Whorls embrace just below the uppermost fine thread on the lower whorl face.

**REMARKS.** *Trinema heideckeri* is superficially resemblant of *Murchisonia* species described below, but is clearly distinguished by the 3 mid-whorl cords and the placement of the sinus. *Trinema* sp. below is differentiated by the position of the suture.

**Trinema sp.**  
(Fig. 5L)

**MATERIAL EXAMINED.** QMF34931.

**DESCRIPTION.** Single fragmentary specimen, high-spired; suture impressed, whorl face dominated by three prominent spiral cords; whorls embrace at lowermost of these; weak spiral thread on uppermost whorl face. Sinus positioned above the highest thick cord. Growth lines fine and numerous.

**REMARKS.** The specimen is distinct from *Trinema heideckeri* sp. nov. in that the whorls embrace higher on the whorl face, at the level of the lower of the three major midwhorl cords. Whether this is an aberrant form or a new taxon is unclear.

Superfamily SUBULITOIDEA Lindstrom 1884  
Family SUBULTIDAE Lindstrom 1884

**Subulites** Emmons, 1842

**?Subulites (Subulites) sp.**  
(Fig. 5M)

**MATERIAL EXAMINED.** QMF34934.

**DESCRIPTION.** Small, high-spired, fusiform shell, 11.3mm high, 4.2mm maximum width, sutures slightly impressed; sutural angle moderate. Whorl profile gently curved. Weak, fine, prosocline, growth lines. Aperture unknown, but shell form suggests presence of anterior notch; inner lip unknown.

**REMARKS.** Questionable assignment is made on the basis of the general shell form, but it cannot be conclusive without data on the columella and the aperture.

**?Subulites (Fusispira) sp. A.**  
(Fig. 5N)

**MATERIAL EXAMINED.** QMF34912.

**DESCRIPTION.** Fusiform, small, rapidly expanding shell, approximately 4mm high and 2mm wide. Whorls embrace just below periphery which is situated just below midwhorl. Whorl profile smoothly rounded. Growth lines, aperture and inner lip unknown.

**REMARKS.** Lack of material prevents accurate assignment of this taxon. It differs from the material described below in having no subsutural angulation.

**?Subulites (Fusispira) sp. B.**  
(Fig. 5O,P)

**MATERIAL EXAMINED.** QMF35517, QMF35518.

**DESCRIPTION.** Small, fusiform, maximum height 4mm, width 2.2mm. Whorl profile rounded except for prominent subsutural surface and angulation high on upper whorl face. Sutures impressed, whorls embrace just below periphery which is slightly below the midwhorl.

**REMARKS.** Inadequate material and poor preservation of lip, ornament and aperture prevents assignment of this material. It differs from *?Subulites (Fusispira) sp. A.* in having a prominent subsutural surface and angulation.

**FAUNAL AFFINITIES**

Presence of species of *Murchisonia*, *Bellerophon* and *Palaeozygopleura*, *Euryzone* and *Anomphalus* demonstrates Old World Realm affinities, but these are at generic level only. It is unclear whether there are links to Chinese and Russian faunas of this age, as they have been so sparingly described, and microgastropods of this age are little-recorded in the literature. There is a general taxonomic continuance with respect to Early Devonian (Emsian) faunas described by Tassell (1982), but this is only on a generic level with the genera represented in both being long-ranging and widespread. Thus there is a strong endemism to the fauna, even when compared to Givetian gastropods from the adjacent Broken River Province (Cook & Camilleri, 1997), with no common species apart from *Burdekinia burdekinensis* and *Labroscuspis nodosa*. This may be a function of the strongly embayed palaeogeographic setting of the Burdekin Subprovince,



in comparison to the open marine conditions of the Broken River Province during the Givetian.

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**PROBABLE PREDATION SCAR ON A DEVONIAN BRACHIOPOD.** *Memoirs of the Queensland Museum* 42(1): 50, 1997:- A silicified pedicle valve of the brachiopod *Warrenella* sp. was recovered from limestone samples of the Burdekin Formation by acetic acid dissolution. The specimen derived from Queensland Museum Locality QML1094, near Little Rocks, Fletcherview Station, and is registered in the Queensland Museum Palaeontology collection QMF35128. Stratigraphy and data concerning the Givetian age of the Burdekin Formation are outlined by Cook (1995).

The valve (Fig. 1) bears a small depression fracture near the right anterior margin, 9mm wide and approximately 2mm deep. This fracture bears a strong resemblance to scars documented in Carboniferous brachiopods by Alexander (1981) and Gutteridge (1989). Alexander (1981) attributes such crushed valves to seized but uningested individuals being grazed upon by sharks. Gutteridge (1989) similarly attributed such scars to predation by sharks.

Given the minimal amounts of vertebrate fossil material recovered from the entire Burdekin Formation (only four incomplete and unidentifiable bone fragments), it is unclear what likely predators could have been responsible for this scar.

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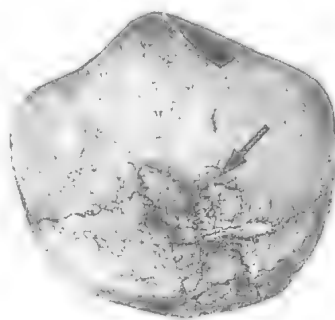


FIG. 1. *Warrenella* sp., QMF35128, arrow indicates probable predation scar, x 1.3. Specimen blackened with colloidal graphite and whitened with ammonium chloride for photography.

Subprovince, north Queensland, Australia. *Memoirs of the Queensland Museum* 38(1): 53-91.

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A.G. Cook, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101; 23 December 1996.

# REVIEW OF FOSSIL GASTROPODS *BURDIKINIA* KNIGHT 1937 AND *AMPHELISSA* ETHERIDGE 1921

ALEX G. COOK

Cook, A.G. 1997 06 30: A review of the gastropod *Burdikinia* Knight 1937 and *Amphelissa* Etheridge, 1921. *Memoirs of the Queensland Museum* 42(1): 51-54. Brisbane. ISSN 0079-8835.

*Burdikinia* is here placed within the Helicotomidae. *Burdikinia axionoides* (Etheridge), from the Middle Devonian of New South Wales is formally included in the genus *Ansterum* Heidecker is a junior synonym of *Amphelissa* Etheridge. □ *Gastropods, Devonian, Helicotomidae*.

Alex G. Cook. Queensland Museum. P.O. Box 3300 South Brisbane Queensland 4101, Australia; 1 May 1997.

The Middle Devonian gastropod *Burdikinia* Knight (1937), with type species *B. burdekinensis* (Etheridge, 1917) is a distinctive, robust, nodose taxon regarded as endemic to northeastern Australia. Erected by Knight (1937) to correct the original assignment of the type species to *Polyamma*, the generic name was a corruption or misspelling of 'Burdekin' either River or Limestone. Despite several studies and reports of *Burdikinia burdekinensis* including taxonomy (Etheridge, 1917; Knight, 1937; Knight, 1941; Heidecker, 1959; Knight et al., 1960) and ecology (Cook, 1993) there has been no conclusion reached on its higher taxonomic placement, partly due to the almost ubiquitous poor preservation of *Burdikinia* specimens. Thus the genus has been relegated to the genera inquirenda (Knight et al., 1960). Discovery of a moderately well-preserved specimen of *B. burdekinensis* finally allows this enigmatic genus to be assigned to a family.

The posthumous publication of Etheridge (1921) of 2 gastropods from the Timor Limestone, Upper Hunter Valley, NSW has been ignored by most studies of Devonian gastropods. Etheridge (1921) erected *Polyamma axionoides* on the basis of 2 worn specimens forwarded to him by the Geological Survey of New South Wales. The only subsequent reference to this taxon is that of Pedder, Jackson & Ellenor (1970) who listed the taxon, assigning the species to '*Burdekinia*' (sic).

Etheridge (1921) also erected *Amphelissa isisensis*, which Pedder, Jackson & Ellenor (1970) listed as *Euomphalus isisensis*. *Ansterum* Heidecker bears striking similarity to *Amphelissa* and is synonymised.

## SYSTEMATIC PALAEOLOGY

Superfamily EUOMPHALIDAE de Koninck, 1881  
Family HELICOTOMIDAE Wenz, 1938

### *Burdikinia* Knight 1937

TYPE SPECIES. *Polyamma burdekinensis* Etheridge 1917 by original designation, from the Middle Devonian (Givetian) Fanning River Group, probably lower Burdekin Formation or Big Bend Arkose.

SPECIES INCLUDED. *Burdikinia burdekinensis* (Etheridge, 1917), Middle Devonian (Givetian), north Queensland; *Burdikinia axionoides* (Etheridge, 1921) from the Middle Devonian (Givetian) Timor Limestone, New South Wales.

DISTRIBUTION. Burdekin Subprovince, N Queensland; Broken River Province, N Queensland; Timor Area, Upper Hunter, New South Wales.

REMARKS. Poor preservation has been the single contributing factor to the lack of understanding of the systematic position of *Burdikinia*. *Burdikinia burdekinensis* occupied high-energy, nearshore environments (Cook, 1993). Consequent abrasion of shell material obliterated all but gross shell detail. Subsequent recrystallisation of much of the available material also obscured taxonomic features, such as the position of the sinus (if any) or selenizone (if any). In addition specimens are usually not conducive to preparation due to the lack of mechanical (and chemical) difference between surrounding matrix and the recrystallised shell.

*Burdikinia axionoides* (Etheridge, 1921) differs from the type species, being more squat, and lacking the prominent cords on the lower whorl face. The lectotype of *B. axionoides*, (Fig. 1D,E) here designated as MMF16014, shows the sinus to be on the flattened upper whorl face, between

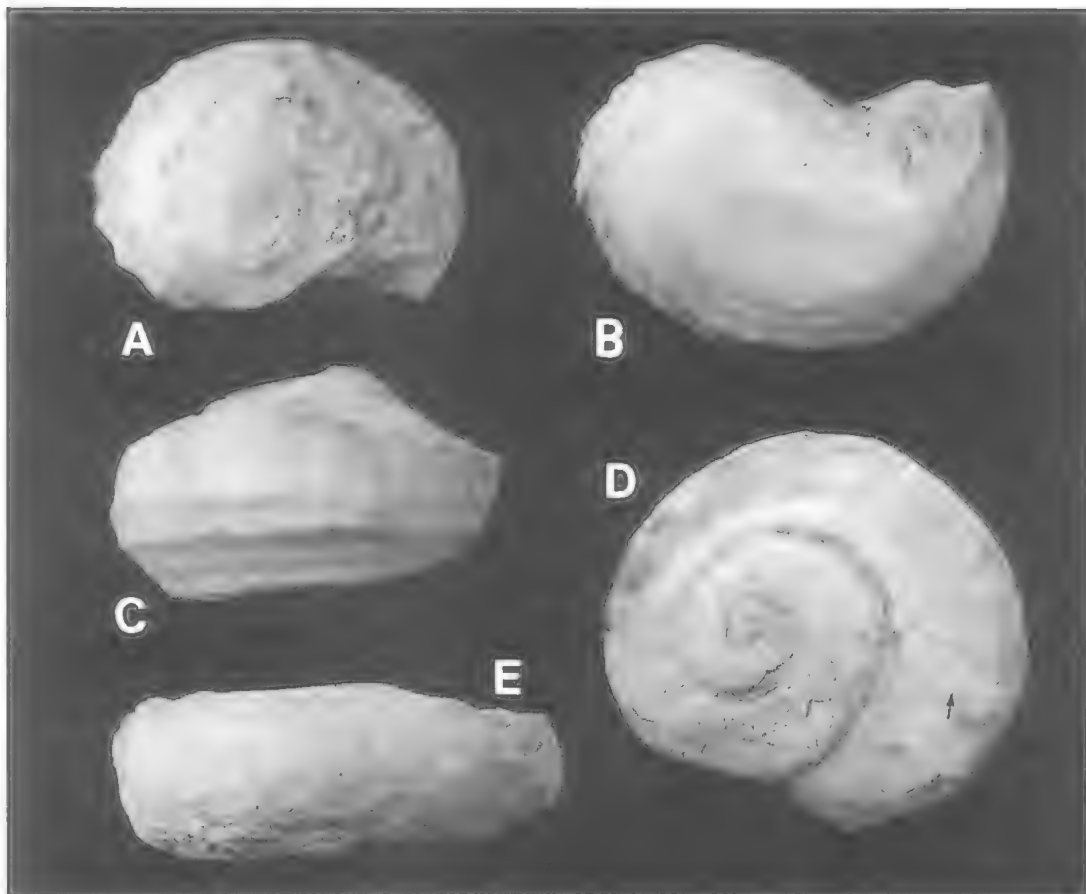


FIG. 1. A-C, *Burdikinia burdekinesis* (Etheridge), QMF35452. A, apical view, arrow shows sinus position, X1; B, side view, X1; C, basal view. D-E, *Burdikinia axionoides* (Etheridge), Lectotype MMF16014 X1. D, apical view, arrow shows sinus; E, side view.

the suture and the nodose cord. The only other specimen of the original suite examined by Etheridge (1921), MMF16015 is poorly preserved and lacks any particular diagnostic features.

*Burdikinia* is here placed in the Helicotomidae because of the dominance of spiral ornament, and particularly the prominent nodose carina bordering the flattened upper whorl surface, and the presence of the shallow sinus on the upper whorl surface between the suture and the bordering carina. The anomphalous base is unlike other Helicotomidae, but reflects great shell thickening as a probable ecological adaptation.

***Burdikinia burdekinensis* (Etheridge, 1917)**  
(Fig. 1A-C)

MATERIAL EXAMINED. HOLOTYPE: GSQF926.  
NEW MATERIAL: QMF35452 from Big Bend, near Charters Towers, NQ.

**ADDITIONAL DESCRIPTION.** See also Etheridge (1917) and Heidecker (1959). Growth lines are fine and numerous; prosocline from the uppermost and peripheral spiral cord, strongly recurved about the base towards the axis; these lines are uninterrupted across the lower whorl surface. The weak sinus is located on the upper whorl face regarded here as a subsutural ramp. The nodes on the spiral cords are solid (as noted by Heidecker) in deference to Knight et al. (1960).

**REMARKS.** The new material places the sinus accurately and refutes any presence of a selenizone.

***Amphelissa* Etheridge 1921**

*Amphelissa* Etheridge 1921: 2; Knight 1941: 34.  
*Austerum* Heidecker 1959: 6.

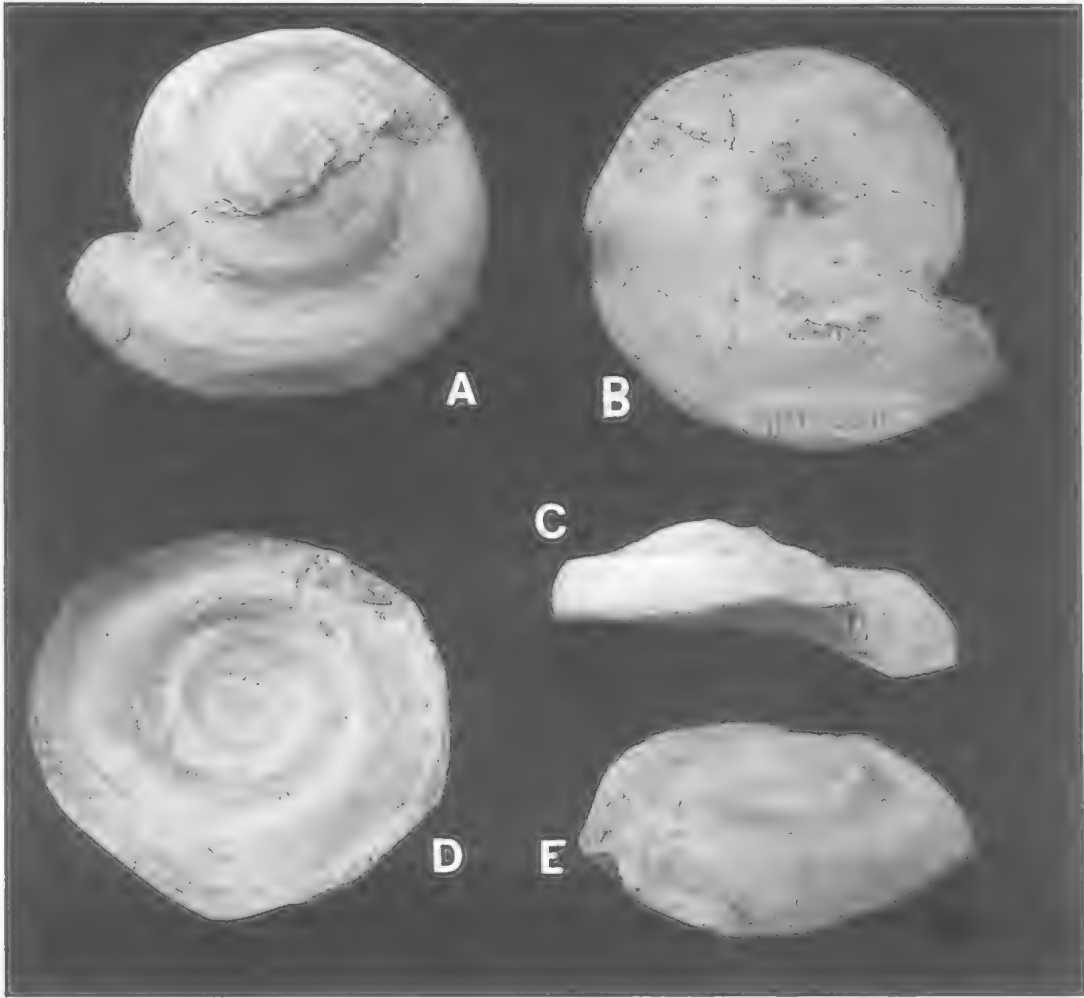


FIG. 2. *Amphelissa isisensis* Etheridge. A-C, Holotype MMF16011, X1, apical, basal and apertural views respectively. D-E, MMF16024, x1. D, apical view; E, side view, note fine growth lines.

**TYPE SPECIES.** By monotypy, *Amphelissa isisensis* Etheridge 1921 from the Middle Devonian Timor Limestone, NSW.

**OTHER SPECIES INCLUDED.** *Amphelissa carinatum* (Heidecker) 1959, from the Middle Devonian Burdekin Formation, north Queensland.

**REMARKS.** *Amphelissa* presented problems to Knight (1941) who was unable to access type materials, due to their misplacement. Consequently, and due to the poor quality of the original illustrations, Knight (1941) regarded the genus as probably widely phaneromphalous. On the holotype of *A. isisensis* (Fig 2A-C) the base is flattened, and the umbilicus is very shallow, wide and

partially plugged by shell, thus hemiomphalus. This is an identical condition to the base of the holotype of *Austerum carinatum* Heidecker. In *A. isisensis* there are well-preserved, fine, numerous growth lines (Fig. 2D,E), which are not preserved on specimens of the north Queensland species.

Heidecker (1959) may have been unaware of the taxon described by Etheridge (1921) from the Timor Limestone which has gone largely ignored. *Amphelissa* was suppressed by Knight et al. (1960), who synonymised it with *Straparollus* (*Euomphalus*). *Amphelissa* Etheridge cannot be accommodated in *Straparollus* (*Euomphalus*) given the hemiomphalus condition. *Amphelissa* is thus resurrected as a valid genus. *Amphelissa carinatum* (Heidecker) differs from the type in

being higher-spined. The holotype of *Amphelissa isisensis*, designated by Knight (1941), is registered in the Geological Survey of New South Wales Collection as MMF16011. The paratypes designated by Knight (1941) are registered under MMF16012.

#### ACKNOWLEDGEMENTS

I am grateful to Dr Ian Percival for loan of material from the Geological Survey of New South Wales collections, to Robert Blodgett for suggestions to the manuscript and to Rae Sheridan for allowing the specimen to leave the educational collections under her control.

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# MIDDLE DEVONIAN GASTROPODS FROM THE BROKEN RIVER PROVINCE, NORTH QUEENSLAND

ALEX G. COOK AND NATALIE CAMILLERI

Cook, A.G. & Camilleri, N. 1997 06 30: Middle Devonian gastropods from the Broken River Province, north Queensland. *Memoirs of the Queensland Museum*, 42(1): 55-79. Brisbane. ISSN 0078-8835.

Twenty seven taxa of gastropods are described from the Eifelian and Givetian sequences of the Broken River Province, north Queensland with four new genera and ten new species. New taxa are *Denayella lomandraensis* sp. nov., *Gyronema simpsoni* sp. nov., *Frillbeastia queenslandicus* gen. et sp. nov., *Brokenriveria pharlapensis* gen. et sp. nov., *Gemininodosa langi* gen. et sp. nov., *Murchisonia* (*Murchisonia*) *wandovalensis* sp. nov., *M. (M.) lawlessi* sp. nov., *Palaeozygopleura dodgeyi* sp. nov., *Australaxa tasselli* gen. et sp. nov. and *Leptogymna queenslandicus* sp. nov. Three gastropod communities are recognised in the Givetian rocks of the province, the *Murchisonia* community, inhabiting a biostromal environment, the *Labrocuspis* community inhabiting high-energy coarse siliciclastic environments and the *Brokenriveria* community inhabiting an open, muddy, carbonate shelf. □ *Gastropods, Givetian, Eifelian, Broken River Province, Queensland.*

Alex G. Cook & Natalie Camilleri. Queensland Museum, PO Box 3300 South Brisbane, 4101, Australia; 1 April 1997.

The Broken River Province, located approximately 200km W of Townsville, north Queensland consists of two subprovinces; Graveyard Creek Subprovince and Camel Creek Subprovince (Withnall & Lang, 1993). The Graveyard Creek Subprovince contains inter alia, a thick, widely-outcropping sequence of Silurian to Middle Devonian, dominantly shallow marine units.

Middle Devonian sequences within the Graveyard Creek Subprovince contain diverse fossil assemblages which have been the subject of intense taxonomic and biostratigraphic study (Jell et al, 1993). Detailed studies of conodonts (Mawson, 1987; Mawson & Talent, 1989; Mawson et al., 1988), fish remains (Turner, 1982, 1995; de Pomeroy, 1994) and corals (Wyatt & Jell, 1967) have provided a substantial biostratigraphic database for taxonomic studies within the province. We follow the summary biostratigraphic scheme presented by Jell et al. (1993).

Until now gastropods have remained unstudied within the Broken River Province. Previous work on Devonian gastropods from north Queensland are Etheridge (1917), Heidecker (1959), and Cook (1993, 1995). Gastropod faunas in south-eastern Australia have received substantially more attention, more recently through the works of Tassell (1976, 1977, 1978, 1980, 1982).

This paper is concerned with gastropods collected from Eifelian and Givetian units of the Broken River Group, namely the Burges Formation, Dosey Limestone and Papilio Mudstone.

Material collected over a number of years by staff at The University of Queensland, Macquarie University and the Queensland Museum contained a small number of gastropods scattered over a large number of localities in the Broken River Province. Subsequent larger collections made by the authors in 1994 and 1995 have revealed a more diverse assemblage. All material is deposited in the Queensland Museum (prefix QMF), and localities are presented in the appendix (QML).

List of Localities. QML541: 'Calceola' stop 6, 2nd creek upstream from Broken River Gorge, Broken River Province, Burges Formation, Eifelian. Collected P.A. Jell. QML1016: Hill above crossing, S side of river near 'PharLap' prospect, Broken River, near old GSQ camp site. 19°28'S, 144°43'E. Papilio Mudstone, Givetian. Collected A. Cook, N. Camilleri. QML1018: Low rise, 1 km S of Storm Dam, 200m W of road at 19°32.92'S, 144°40.51'E. Papilio Mudstone, Givetian. Collected A. Cook, N. Camilleri. QML1019: Ridge of silicified (silerete)-replaced Dosey Limestone, 100m north of road 500m E of Storm Dam 190. QML1083, Nuggety Gully, E of Gorge-PharLap Rd, basal Papilio Mudstone, just above and adjacent to top of N most Dosey Limestone, 19°27.79'S, 144°44.86'E. Papilio Mudstone, Givetian. Collected A. Cook, N. Camilleri, P. Lawless, D. Case, S. Dodgey-Hocknull, P. Dodgey-Tierney, R. Lootsma, 1995: QML1090. Above 'PharLap' crossing on Broken River, N side of River on washed out track approx. 400m NE of QML1016. 19°28.71S, 144°44.05'E.

Papilio Mudstone, Givetian. Collected QM Party 1995. QML1092: 500m NW of type section creek for Dosey & Lomandra Limestones. 150m above Dosey Limestone. 19°29.98'S, 144°43.87'E. Papilio Mudstone, Givetian. Collected QM Party July 1995. A. Cook, P. Lawless, C. McHenry, September 1995. SD21: E side of Dosey Syncline in tributary of Dosey Creek. (see Mawson & Talent, 1989; 221) Papilio Mudstone, Givetian. SD43e: Storm Dam area, Papilio Mudstone, Givetian. SD108: Approx 1.5km NE of Spanner Hill, Papilio Mudstone or Lower Mytton Formation. (see Mawson & Talent 1989: 211) Givetian.

### GASTROPOD ASSEMBLAGES

Three Givetian gastropod communities are recognised; *Labroscuspis* community, *Brokenriveria* community and *Murchisonia* community (Table 1), corresponding to differing sedimentologic regimes. The *Labroscuspis* community is found in conglomerates and coarse sandstones interpreted as high energy facies at the basal Papilio Mudstone near 'Nuggetty Gully' area and from similar sandstones in the uppermost Papilio Mudstone or lowermost Mytton Formation in the 'Spanner Hill' area. This occurrence is strikingly similar to the *Burdikinia-Labroscuspis-Asterum* faunule noted by Cook (1993), which occurs in high energy nearshore facies of the Big Bend Arkose (Givetian, Burdein Subprovince).

*Brokenriveria* community occurs within carbonate mudstone facies of the Papilio Formation, interpreted as shallow, low energy, open marine, impure carbonate shelf. *Murchisonia* community is derived from within the uppermost Dosey Limestone and is associated with corals, stromatoporoids, sponges from a biostromal environment.

Eifelian gastropods are insufficiently represented in the collected fauna to comment on their community arrangement.

### FAUNAL AFFINITIES

Comment has already been made on the similarity of *Labroscuspis* community in the Burdekin Subprovince and the Broken River Province. In both are also found the bivalve *Tanaodon louderbacki*, which is also known from the Givetian of Guangxi (Pojeta et al., 1985). The presence of *Murchisonia* species, *Soleniscus*, palaeozygopleurids and *Platyceras* suggests affinity with Old World Realm faunas, but sufficiently removed to develop distinct endemism at the

TABLE 1. Constituent taxa of Givetian gastropod communities. r = rare, c = common, a = abundant, s = single occurrence.

Species	<i>Murchisonia</i> community	<i>Labroscuspis</i> community	<i>Brokenriveria</i> community
<i>Bellerophon</i> ( <i>Bellerophon</i> ) sp. A.			s
<i>Bellerophon</i> ( <i>Bellerophon</i> ) sp. B.			s
<i>Straparollus</i> ( <i>Straparollus</i> ) sp.	s		
<i>Straparollus</i> ( <i>Euomphalus</i> ) sp. A	r		
<i>Straparollus</i> ( <i>Euomphalus</i> ) sp. B	s		
<i>Labroscuspis nodosa</i> Heidecker		c	
<i>Omphaoltrochid</i> indet.	s		
<i>Denayella lomandraensis</i> sp. nov.			r
<i>Frillbeastia queenslandicus</i> gen. et. sp. nov.	r		
<i>Brokenriveria pharlapensis</i> sp. nov.			a
<i>Gemininodosa langi</i> gen. et sp. nov.			a
<i>Platyceras</i> ( <i>Platyceras</i> ) sp.			s
<i>platyceratoid</i> indet.			s
<i>Burdikinia burdekinensis</i> (Etheridge)		r	
<i>Murchisonia</i> ( <i>Murchisonia</i> ) <i>wandovalensis</i> sp. nov.			c
<i>Murchisonia</i> ( <i>Murchisonia</i> ) <i>lawlessi</i> sp. nov.	c		
<i>Murchisonia</i> ( <i>M.</i> ) sp. cf. <i>M. (M.) fermioni</i> Tassell	c		
<i>Murchisonia</i> ( <i>M.</i> ) sp.	s		
<i>murchisoni</i> indet.	r		
<i>Stylonema?</i> sp.	s		
<i>Australoxa tasselli</i> gen. et sp. nov.			r
<i>Palaeozygopleura dodgeyi</i> sp. nov.			r
<i>Soleniscus</i> sp. cf. <i>S. subcostata</i> Schlotheim	r		
<i>Leptogymna queenslandicus</i> sp. nov.			c
<i>Mitchellia striatula</i> de Koninck			s

species level. There are, however closely related species of *Brokenriveria* gen. nov. and possibly *Frillbeastia* gen. nov. known from Germany as argued below. There are other generic level affinities with Eifelian faunas in Nevada (Blodgett, 1992) and Alaska (Blodgett & Johnston, 1992) and Givetian faunas in Yunnan (Mansuy, 1912), Guangxi (Wei & Pan, 1988). Taxonomic hangovers from southeastern Australian faunas of Emsian age are evidenced by the co-occurrence of *Mitchellia*, *Leptogymna*, and *Murchisonia* (*M.*) sp. cf. *M. (M.) fermioni* Tassell. A dearth of taxonomic work on southeast Asian and Russian gastropods of Middle Devonian age makes conclusive assessment of the taxonomic affinities impossible.

## SYSTEMATIC PALAEOLOGY

Class GASTROPODA Cuvier, 1797  
 Order ARCHAEOGASTROPODA Thiele, 1925  
 Superfamily BELLEROPHONTOIDEA  
 M'Coy, 1851  
 Family BELLEROPHONTIDAE M'Coy, 1851  
*Bellerophon* Montfort, 1808  
*Bellerophon* (*Bellerophon*) Montfort, 1808

*Bellerophon* (*Bellerophon*) sp. A.  
 (Fig. 1A, B)

MATERIAL EXAMINED. QMF32642 from SD21.  
 QMF32644 from QML1018.

DESCRIPTION. Medium-sized, isostrophic shell, up to 20mm wide and 20mm diameter; doubly phaneromphalous. Whorl profile gently rounded, with a weak ridge mid-whorl. Smooth, fine, growth lines, nearly straight; shell rapidly expanding; lip and aperture unknown.

REMARKS. Poor preservation of this material does not allow confident specific assignment to one of the many species of *Bellerophon* (*Bellerophon*). It is assigned to this subgenus on the basis of the rounded whorl profile, absence of spiral ornament and simplicity of growth lines.

*Bellerophon* (*Bellerophon*) sp. B  
 (Fig. 1C, D)

MATERIAL EXAMINED. QMF33621 from QML1092.

DESCRIPTION. Small, isostrophic shell, 10mm wide, 10mm diameter; rapidly expanding, aperture flared. Selenizone, prominent upon weak ridge. No growth lines preserved.

REMARKS. The single, poorly preserved specimen cannot be assigned to a species. It is more rapidly expanding and smaller than *Bellerophon* (*Bellerophon*) sp. A.

Superfamily EUOMPHALOIDEA  
 de Koninck, 1881  
 Family EUOMPHALIDAE de Koninck, 1881  
*Straparollus* de Montfort, 1810  
*Straparollus* (*Straparollus*) de Montfort, 1810

*Straparollus* (*Straparollus*) sp.  
 (Fig. 1E, F)

MATERIAL EXAMINED. QMF33103 from QML1019.

DESCRIPTION. Medium-sized, trochiform shell, approximately 5.5mm high, 10mm wide; apical angle approximately 110°, sutures strongly impressed. Whorl profile strongly rounded with slight shoulder. Ornament consists of numerous fine growth lines, slightly prosocline. There is a very slight flexure in the growth lines on the weak shoulder suggesting the sinus. Just below mid-whorl near the aperture, there is an apparent shell repair.

REMARKS. The specimen is confidently assigned to the subgenus on the basis of the whorl profile, overall shape and ornament. The number of species of this subgenus is large and confident assignment to species is unwise due to the lack of material, and the degree of variation present in known taxa (Linsley & Yochelson, 1973). The specimen differs from *S. (S.) ater* (Spitz) of Jhaveri (1969) from the lower Devonian of the Carnic Alps, which is much more squat. *S. (S.) kokeni* (Spitz) of Jhaveri (1969) has a much more prominent shoulder. Of the taxa described by Linsley & Yochelson (1973), *S. (S.) laevis* (Archiac & Vermeuil), from the Middle Devonian of Germany, is more flattened, but their *S. (S.) ?laevis* is more resemblant of the Broken River specimen. *S. (S.) cyclostomus* (Hall) of Linsley & Yochelson (1973) from the Middle Devonian of North America has a more prominent sinus.

*Straparollus* (*Euomphalus*) Sowerby, 1814

*Straparollus* (*Euomphalus*) sp. A  
 (Fig. 1G)

MATERIAL EXAMINED. QMF33104, QMF33352 from L1019.

DESCRIPTION. Small, planispiral shell up to 12mm in diameter, 4mm maximum height. Both specimens are preserved as basal moulds. Whorl profile subrounded to subquadrate, with a weak angulation between the midwhorl and basal surfaces obvious in the last whorl. No obvious growth lines preserved, but there is a faint hint of fine collabral lines on QMF33104. Protoconch unknown.

REMARKS. This material cannot be identified further due to inadequate preservation.

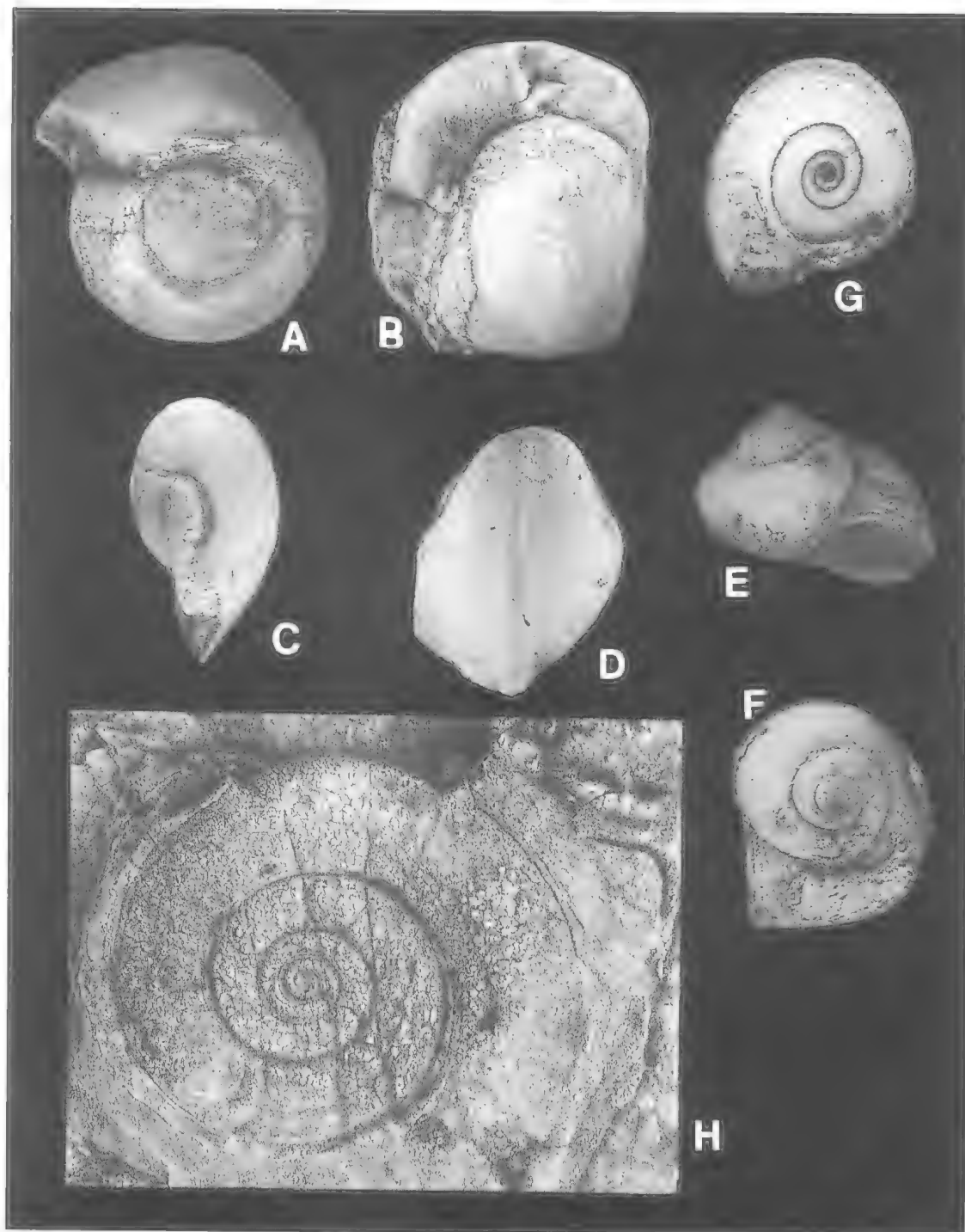


FIG. 1. A,B, *Bellerophon* (*Bellerophon*) sp. A., QMF32642 x 2.2. A, side view; B, apertural view. C,D, *Bellerophon* (*Bellerophon*) sp. B., QMF33621 x 2.7. C, side view; D, view of selenizone. E,F, *Straparollus* (*Straparollus*) sp., latex moulds from QMF34267 x 3.1. E, apertural view; F, apical view. G, *Straparollus* (*Euomphalus*) sp. A., QMF33352 x 3.1, basal view. H, *Straparollus* (*Euomphalus*) sp. B., QMF34752 x 2.2. All specimens (and those on subsequent figures) whitened with ammonium chloride for photography.

**Straparollus (Euomphalus) sp. B.**  
(Fig. 1H)

MATERIAL EXAMINED. QMF34752 from QML1018.

DESCRIPTION. Large, planispiral, 42mm in diameter; 4 whorls preserved in cross section and external mould, the first 2 preserved whorls are septate; septa gently concave; collabral growth lines preserved on the final whorl are fine and numerous.

REMARKS. The planispiral form, simplicity of growth lines and the septation identifies the subgenus, but a species cannot be assigned.

Family OMPHALOTROCHIDAE  
Knight, 1945

**Labrocuopsis** Heidecker, 1959

*Labrocuopsis* Heidecker, 1959: 6; Kase, 1989: 149.

TYPE SPECIES. *Labrocuopsis nodosa* Heidecker, 1959, by original designation, from the Middle Devonian (?late Eifelian- Givetian), Big Bend Arkose, north Queensland.

DIAGNOSIS. Large, anomphalous trochiform gastropod; suture deep and impressed, whorl profile rises from the suture to a keel and descends to a variably developed peripheral buttress.

REMARKS. *Labrocuopsis* is presently restricted to two taxa; the type and *L. kobayashii* (Kase & Nishida, 1988), from the Eifelian Nakazato Formation, north east Japan. Kase (1989) assigned the genus to Omphalotrochidae. Heidecker (1959) remarked on the differential development of the peripheral buttress, it only being fully expressed in larger forms.

Occurrences of the genus recorded by Heidecker (1959), Kase (1989) and Cook (1993) highlight association of this genus with nearshore to shoreline, often high energy siliciclastic deposition. Cook (1993) suggested strong ecological control for the genus within the Big Bend Arkose and Burdekin Formation. Material here described is from coarse-grained siliciclastic units, including conglomerates and very coarse to granular sandstones which display cross and planar lamination. Thus a high-energy shallow water environment is suggested.

**Labrocuopsis nodosa** Heidecker, 1959.  
(Fig. 2A-C)

*Labrocuopsis nodosa* Heidecker, 1959: 6, Pl. 1 fig. 2a-d, Pl. 3, fig. 2a-b.

MATERIAL EXAMINED. QMF16547, QMF33316 locality imprecise, Broken River Province, collected M. Wade. QMF33315 from SD108, Upper Papilio Formation or Mytton Formation, collected J. Jell. QMF33582 from QML1089; QMF33580, QMF33581, QMF33583 from QML1083. There is some doubt as to the exact origin of specimens QMF16547, QMF33315 and QMF33316. All were collected at the same time, with J. Jell (pers. comm.) recording the origin as Locality SD108, within the Papilio Formation. However the coarser grained lithology would suggest the nearby outcrops of Mytton Formation.

DISTRIBUTION. Middle Devonian (?late Eifelian- Givetian), north Queensland. The species is apparently endemic to the region. Very poorly preserved material from the Laroona Formation, Burdekin Subprovince may belong to this taxon, which would extend the age range to the Emsian.

DESCRIPTION. Moderately large, thick-shelled, dextrally-coiled, trochiform gastropod up to 63mm high and 36mm wide, with an apical angle up to 120°; suture deep and impressed; sutural slope approximately 10°. Whorl profile rises sharply from the suture to a gently rounded carina, and slopes to a very gently convex profile. Upper whorl profile is gently convex, but breaks midwhorl to produce a gently concave profile below the midwhorl producing a buttress on the lowermost surface. The carina is conspicuously nodose particularly in final whorls. Base flat, with a wide callus pad. Aperture quadrate. Growth lines preserved on base, none preserved on whorl surface.

REMARKS. *Labrocuopsis nodosa* was only previously recorded in the nearby Burdekin Subprovince, Givetian, north Queensland (Heidecker, 1959). The Broken River material is relatively poorly preserved but is inseparable from *L. nodosa* Heidecker from the Big Bend Arkose and Burdekin Formation, having the nodose carina, variable development of the buttress, and strongly developed callus pad. It differs from *L. kobayashii* (Kase & Nishida) in the degree of sutural impression, the nodose carina, and hence the upper whorl profile.

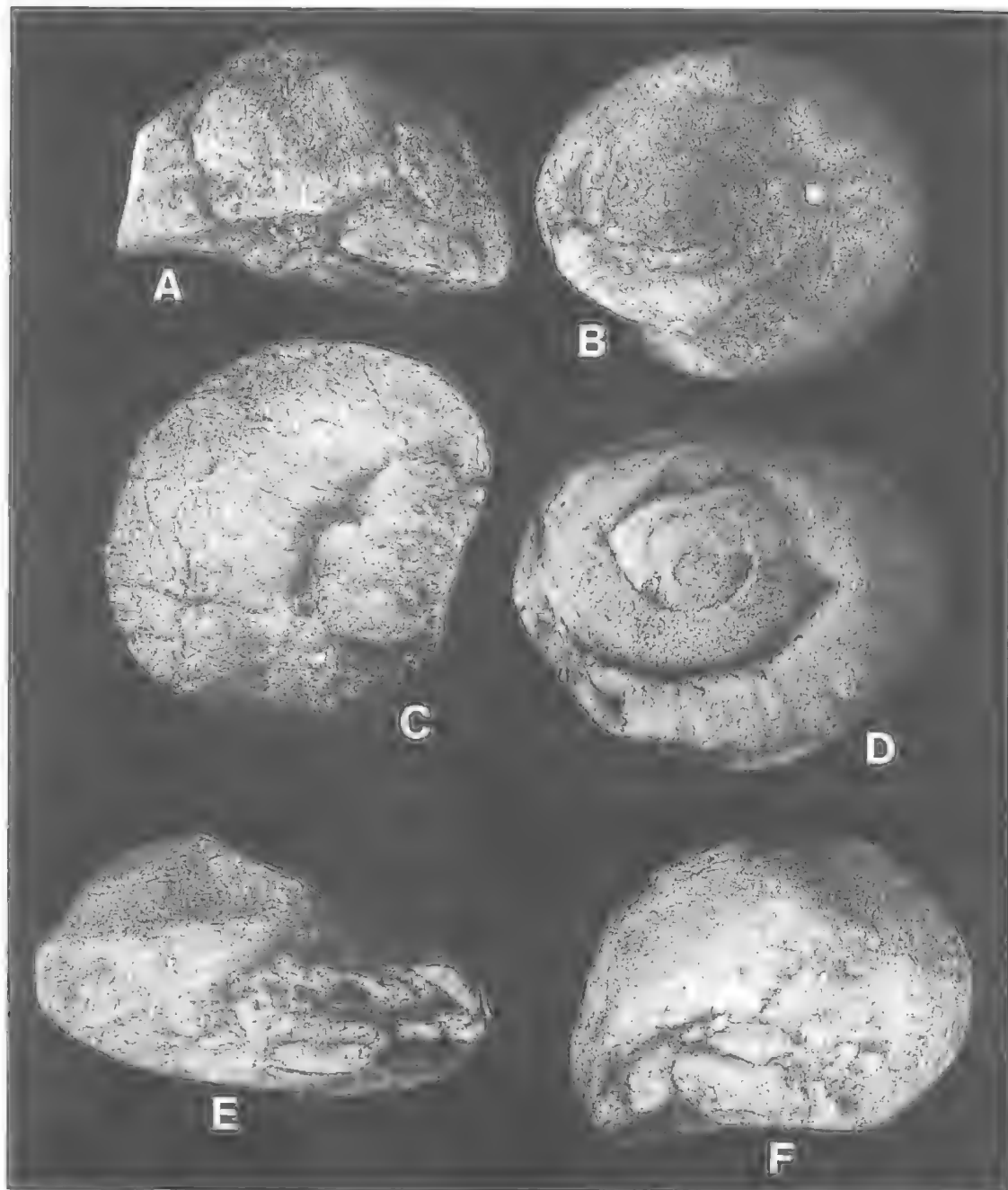


FIG. 2. A-C, *Labroscuspis nodosa* Heidecker, 1959, QMF33583 x 1, apertural, apical and basal views respectively. D, Omphalotrochid indet., latex mould from QMF33687 x 2, apical view. E,F, *Burdkininia burdekininnsis* (Etheridge, 1917), QMF33579 x 2. E, apertural view. F, apical view.

Omphalotrochid indet.  
(Fig. 2D)

MATERIAL EXAMINED. QMF33687 from QML1019.

DESCRIPTION. Mould of an upper surface of a large, shallowly trochiform shell, 25mm in diameter. Apical angle approximately 140°. Suture deep, impressed forming a channel in last whorl. Growth lines fine, collabral.

REMARKS. The specimen superficially resembles *Oreocopia murrayi* Tassell, 1978 from the Lower Devonian Bell Point Limestone, Victoria, but cannot be confidently assigned to a genus as no basal structures are known. The specimen lacks the nodose carina of *Labroscuspis nodosa* Heidecker. The specimen is left in open nomenclature pending more material.

Superfamily PLEUROTOMARIOIDEA  
Swainson, 1840

Family RAPHIStOMATIDAE Koken, 1896  
Subfamily RAPHIStOMATINAE Koken, 1896

*Denayella* Blodgett & Johnson, 1992

TYPE SPECIES. *Denayella housei* Blodgett & Johnson, 1992, from the Eifelian Denay Limestone of Nevada, U.S.A

*Denayella lomandraensis* sp. nov.  
(Fig. 3 A,B)

MATERIAL EXAMINED. HOLOTYPE: QMF33650 from QML1092, Papilio Mudstone, Givetian, Broken River Province. PARATYPES: QMF33651-33672, QMF34215-34222 from QML1092, QMF33619 from QML1090.

DIAGNOSIS. Small member of genus with flattened base and weak inductural deposit.

DESCRIPTION. Small (Table 2) lenticular, omphalus. Whorl profile sharply rounded, upper surface gently sloping, lower surface steeper. Periphery on upper 1/3 of whorl profile, sharply rounded bearing 2 indistinct cords delimiting a probable selenizone, within which the lunulae are not preserved. Lower cord is more obscure than the upper and on many specimens they are not preserved due to abrasion. Aperture rhomboid to subrounded, with a v-shaped sinus on the labrum. Shell thick especially at columella. There is a distinct thickening of shell on the columella. Base convex, but not sharply so. Very weak, fine, col-

TABLE 2. Measurements for *Denayella lomandraensis* sp. nov.

Specimen	height (mm)	width (mm)
QMF33650	4.3	7.0
QMF33651	4.3	6.7
QMF33652	3.8	6.1
QMF33655	4.1	7.4

labral growth lines, otherwise surface smooth and unornamented.

REMARKS. The material is placed in *Denayella* due to its raphistomid-like appearance, indistinct, but present, selenizone and weak inductural deposit on the columellar lip. It differs from the type species in having a more flattened base and a weaker deposit on the columellar lip. It is more similar to *Denayella* sp. of Blodgett & Johnson, 1992 with respect to the flatter base. The species differs from members of *Arizonella* Stoyanow, 1948 by its lack of a prominent selenizone, and well developed collabral ornament. It differs from *Buchelia* and *Raphistoma* due to the lack of cords on the upper whorl face. *Umbotropis mesoni* Tassell 1982, from the *Receptaculites* Limestone of New South Wales is clearly phaneromphalus, and has more prominent spiral cords on the upper whorl face rather than the periphery.

ETYMOLOGY. For Lomandra Creek.

Subfamily LIOSPIRINAE Knight, 1956

*Frillbeastia* gen. nov.

DIAGNOSIS. Small, trochiform with flattened base; angular periphery with selenizone bounded below by frilled carina; upper whorl face with 2 strong threads, the lowermost of which is nodose; strong prosocline ornament; planispiral protoconch.

TYPE SPECIES. *Frillbeastia queenslandicus* sp. nov.

DISTRIBUTION. Middle Devonian (Givetian), uppermost Doscy Limestone, Broken River Province, north Queensland, ?Middle Devonian (Givetian), Germany (Sandberger & Sandberger, 1850-6).

REMARKS. The genus is similar to *Arastra* Stoyanow, 1948 from the early Late Devonian in Arizona, having a distinct frill, but is less lenticular in shape, possesses stronger collabral ornament, strong spiral cords with nodes, and the



protoconch is planispiral. Superficially similar is *Astralites* Whiteaves, 1892 from the Middle Devonian of Canada, which lacks the prominent selenizone and spiral ornament. Members of the *Luciellidae* Knight, 1956 such as *Luciella* de Koninck, 1883 and *Epiptychia* Perner 1907 have the frill above the selenizone, rather than below in *Liospirinae*. *Zalozone* Linsley, 1968 possesses a double frilled selenizone, and *Tylozone* Linsley, 1968 has a selenizone bordered by an upper frill. *Frillbeastia* is placed in *Liospirinae* due to closer similarity to *Arastra*, but is by far the most trochiform member of the subfamily. Linsley (1968) placed *Arastra* within the *Raphiostomatinae*, with *Zalozone*. The base of *Frillbeastia* is wide and hence is retained in *Liospirinae* with the wide-based *Arastra*.

Within the genus could be included *Littorina alata* Sandberger & Sandberger, 1850-1856 from the Middle Devonian (Givetian) of Germany. The taxon illustrated (Sandberger & Sandberger, 1850-56: pl. 24: fig. 14) shows the characteristic frilled keel, a similar base, and numerous cords on the upper surface. It differs from *F. queenslandicus* by having numerous equal strength cords, it lacks the strong growth lines and the nodose cord above the selenizone which is not identifiable on the illustrations of the German taxon.

ETYMOLOGY. For the informal name given in the field, reflecting the character of the selenizone.

***Frillbeastia queenslandicus* sp. nov.**  
(Fig. 3C-G)

MATERIAL EXAMINED. HOLOTYPE: QMF33687, from QML1019 uppermost Dosey Limestone Givetian, Broken River Province. PARATYPES: QMF33695, QMF34265 from QML1019.

DIAGNOSIS. As for genus.

DESCRIPTION. Small, trochiform, nearly conical shell, complete specimen is 16mm wide, 11mm high with a spire angle of approximately 60°. Base flattened, bearing spiral cord, narrowly phaneromphalus or anomphalous. Whorl face ornate and angular with suture just below frill on midwhorl. Upper whorl face possesses 2 major threads, 1 close to the periphery, and another weaker thread on the mid-upper whorl face. These increase in strength throughout growth. The lowermost thread possesses stout rounded nodes, the upper thread has vestigial nodes preserved on the holotype. The angular shell periphery is decorated by a simple, fine spiral thread which is the upper boundary for the selenizone.

Below the selenizone is bordered by a rhythmically folded carina, thus producing a frill. The lower whorl profile possesses a single thread, slightly nodose. Collabral ornament is prosocline. Protoconch nearly planispiral, 2-3 whorls with simple comarginal ornament; a vestige of a selenizone is recognisable on the 3rd whorl.

REMARKS. Despite the small number of specimens the material is significantly distinct to warrant erection of a new genus. One of the specimens has less distinct nodes and cords on the upper whorl face, and shows signs of abrasion.

ETYMOLOGY. For the state of Queensland.

Suborder TROCHINA Cox & Knight, 1960  
Superfamily PLATYCERATOIDEA Hall, 1859  
Family HOLOPEIDAE Wenz, 1938  
Subfamily GYRONEMATINAE Knight, 1956

***Gyronema* Ulrich in Ulrich & Scofield, 1897**

TYPE SPECIES. *Trochonema* (*Gyronema*) *pulchellum* Ulrich and Scofield, 1897 from the Middle Ordovician, Minnesota, United States of America.

DIAGNOSIS. See Knight et al. (1960).

***Gyronema simpsoni* sp. nov.**  
(Fig. 4C,D)

MATERIAL EXAMINED. HOLOTYPE: QMF32082 from QML541. Burges Formation, Eifelian, Broken River Province. PARATYPES: QMF32055, QMF32058 from QML541.

DIAGNOSIS. Very large *Gyronema* with characteristic thickened spiral cords, flattened uppermost whorl surface forming a low shoulder, 2 prominent cords on upper whorl surface, the highest being an angular carina, 6 prominent cords on final whorl.

DESCRIPTION. Large, turbiniform, narrowly phaneromphalus gastropod, with prominent thick spiral ornament and impressed sutures. Shell height up to 47mm, and width up to 32mm, with an apical angle of approximately 20°. External whorl profile is dominated by spiral cords, the uppermost forming a prominent angular carina high on the whorl profile which is divided into two surfaces. Uppermost third of the whorl profile is a gently concave shoulder, which slopes shallowly from the suture to the carina; mid whorl is nearly vertical, and the lower whorl profile gently convex with both marked by thick spiral cords. Sutures formed at midwhorl, slightly

above the 3rd spiral cord, thus obscuring all but 2 uppermost cords on early whorls. Aperture generally rounded, slightly vertically extended with abaxial angulation above midwhorl. Growth lines unknown. The 2 paratypes are somewhat crushed and distorted, but retain the characteristic spiral cords.

**REMARKS.** Material has the typical form of the genus, but differs from the type species by the more flattened shoulder, in addition this taxon is several times larger than the genotype figured by Knight (1941). In size and form this species is comparable to *G. bellense* of Tassell from the Early Devonian of Victoria but *G. bellense* has far more numerous spiral cords. *G. lirata* (Hall) of Rollins, Eldredge & Spiller (1971), from the Middle Devonian Marcellus Formation, New York is smaller (17mm high), with more spiral cords on the upper whorl surface, however it does possess a similar shoulder to *G. simpsoni*. *Gyronema scaliforme* Zytlenok, 1976 from the Devonian of Belorus' possesses more cords than the Broken River species. The species is close to *G. ormistoni* Blodgett, 1992 from the Eifelian of Alaska, but lacks the prominent basal cords of that taxon.

**ETYMOLOGY.** For Andrew Simpson.

**Brokenriveria** gen. nov.

**TYPE SPECIES.** *Brokenriveria parlapensis* sp. nov.

**DIAGNOSIS.** Small turritiform gyronematid with 2 orders of nodose spiral cords.

**DISTRIBUTION.** Middle Devonian (Givetian) Papilio Mudstone, Broken River Province, north

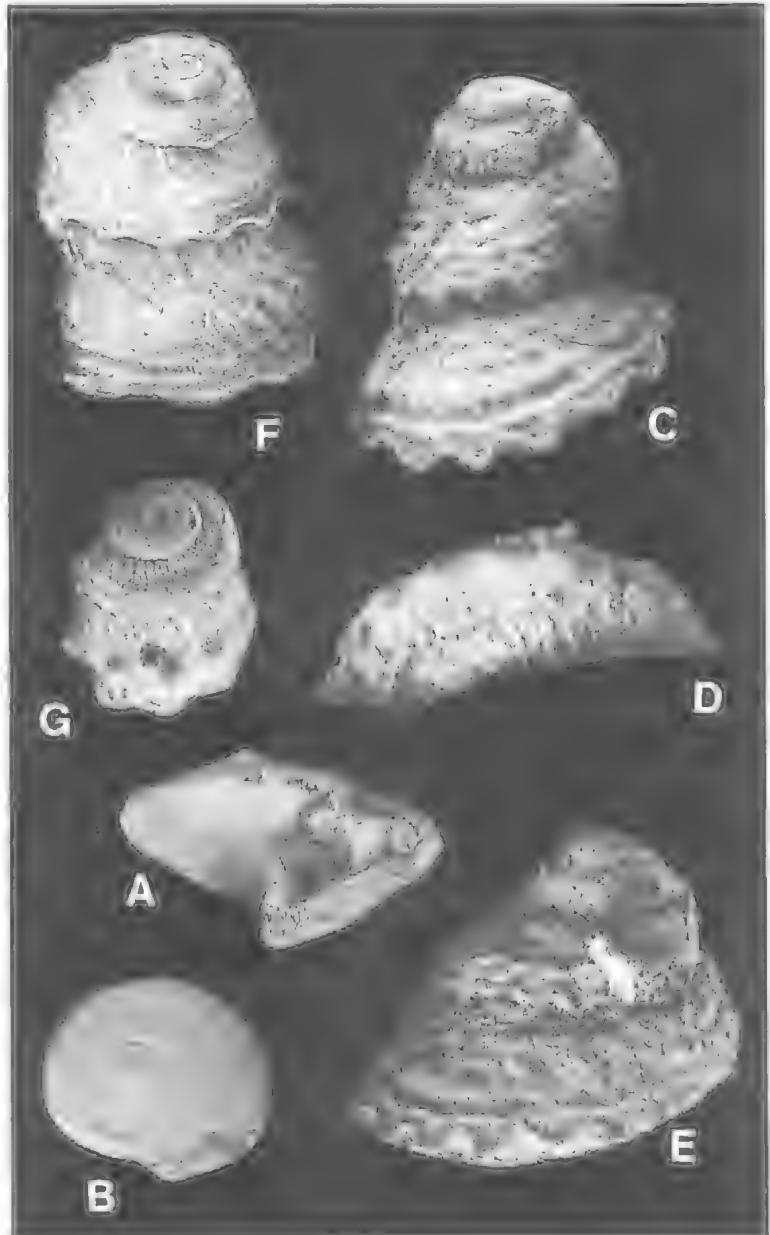


FIG. 3. A, B, *Denayella lomandraensis* sp. nov., Holotype QMF33650 x 6. A, apertural view; B, apical view. C-E, *Frillbeastia queenslandicus* gen. et sp. nov. C-E, latex mould of Holotype QMF33687 x 3.6. C, oblique side view; D, basal view; E, side view. F, latex mould of Paratype QMF34265, x 3.1, side view. G, latex mould of Paratype QMF33695, x 4.5, oblique view showing protoconch.

Queensland, Middle Devonian, Rhineland (Goldfuss, 1844).

**REMARKS.** Lack of a selenozone precludes assignment of this material to grossly similar genera

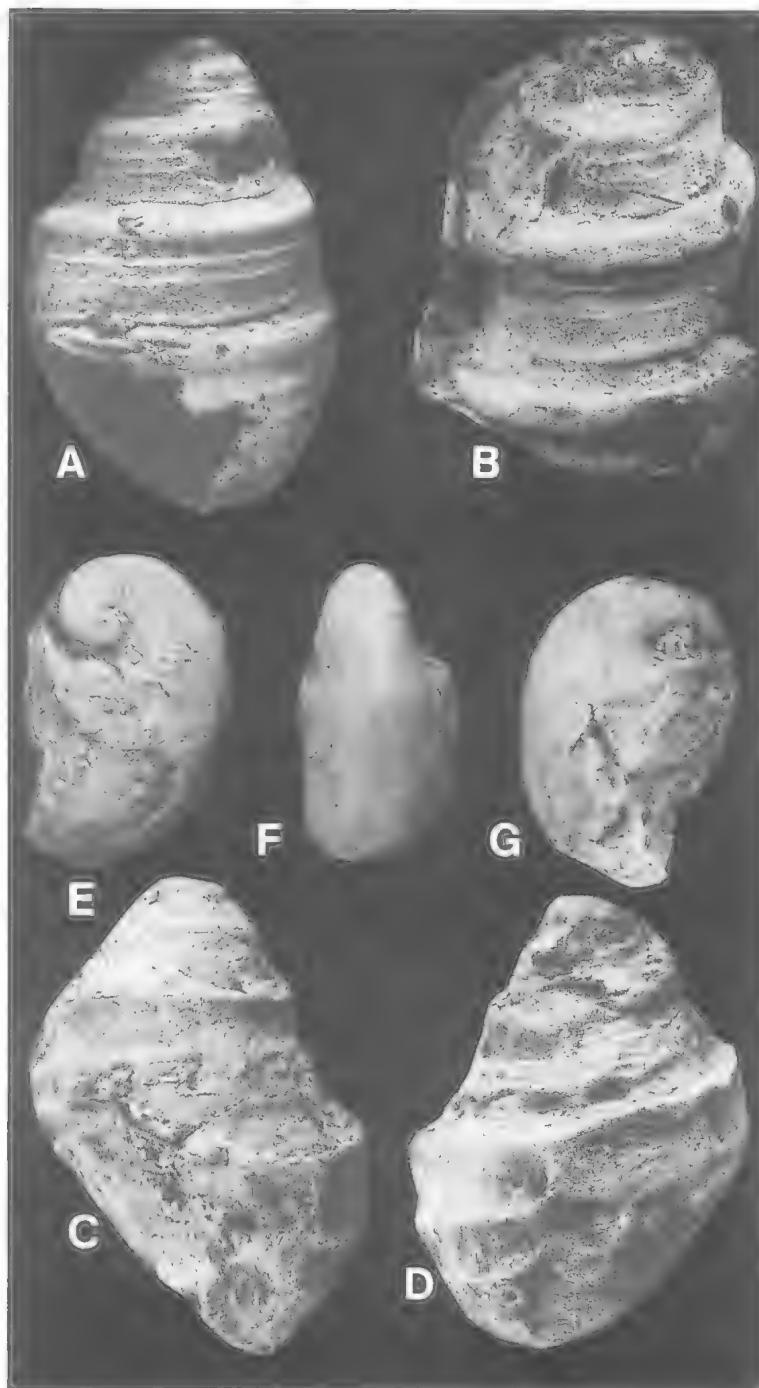


FIG. 4. A, B. Murchisoniind indet. A, latex mould of QMF33100, side view x 1.8. B, latex mould of QMF34259, oblique side view x 2.7. C, D. *Gyronema simpsoni* sp. nov. Holotype QMF32082, x 1.3. C, apertural view; D, side view. E-G, *Platyceras* (*Platyceras*) sp. QMF32641, x 2.7. E, apical view; F, side view; G, basal view.

*Bembexia* Oehlert, *Nodonema* Linsley, or other Pleurotomarioidea. The prosocline growth lines across the shell, the strong cords and the thicker shell suggest that this material can be accommodated within the Gyronematidae. The genus differs from other gyronematids in the possession of two orders of spiral cord, rather than one on *Yunnanina* Mansuy, and *Gyronema* Ulrich. Robert Blodgett (pers. comm) has kindly drawn my attention to a similarly ornamented taxon *Turbo caelatus* Goldfuss, 1844 from the Middle Devonian of Germany, which should be included in the genus, but differs in the number of cords on the upper whorl face.

ETYMOLOGY. For the Broken River.

***Brokenriveria pharlapensis*  
sp. nov. (Fig. 5)**

MATERIAL EXAMINED. HOLOTYPE: QMF32234 from QML1016, Papilio Mudstone, Givetian, Broken River Province. PARATYPES: QMF32235-32301 from QML1016.

DIAGNOSIS. As for genus.

DESCRIPTION. Small to medium-sized, turbiniform gastropod, up to 17mm high and wide (Table 3) with an apical angle of approximately 105°. Whorl profile rounded, but dominated by two orders of numerous nodose spiral cords. Suture impressed, whorls embrace at the midwhorl. Periphery situated at midwhorl. Six major threads on the whorl surface, 1 on the upper whorl face, another at midwhorl, the remainder on the lower whorl face. Major cords are interspaced with 1 less prominent nodose spiral thread, with the exception of the uppermost

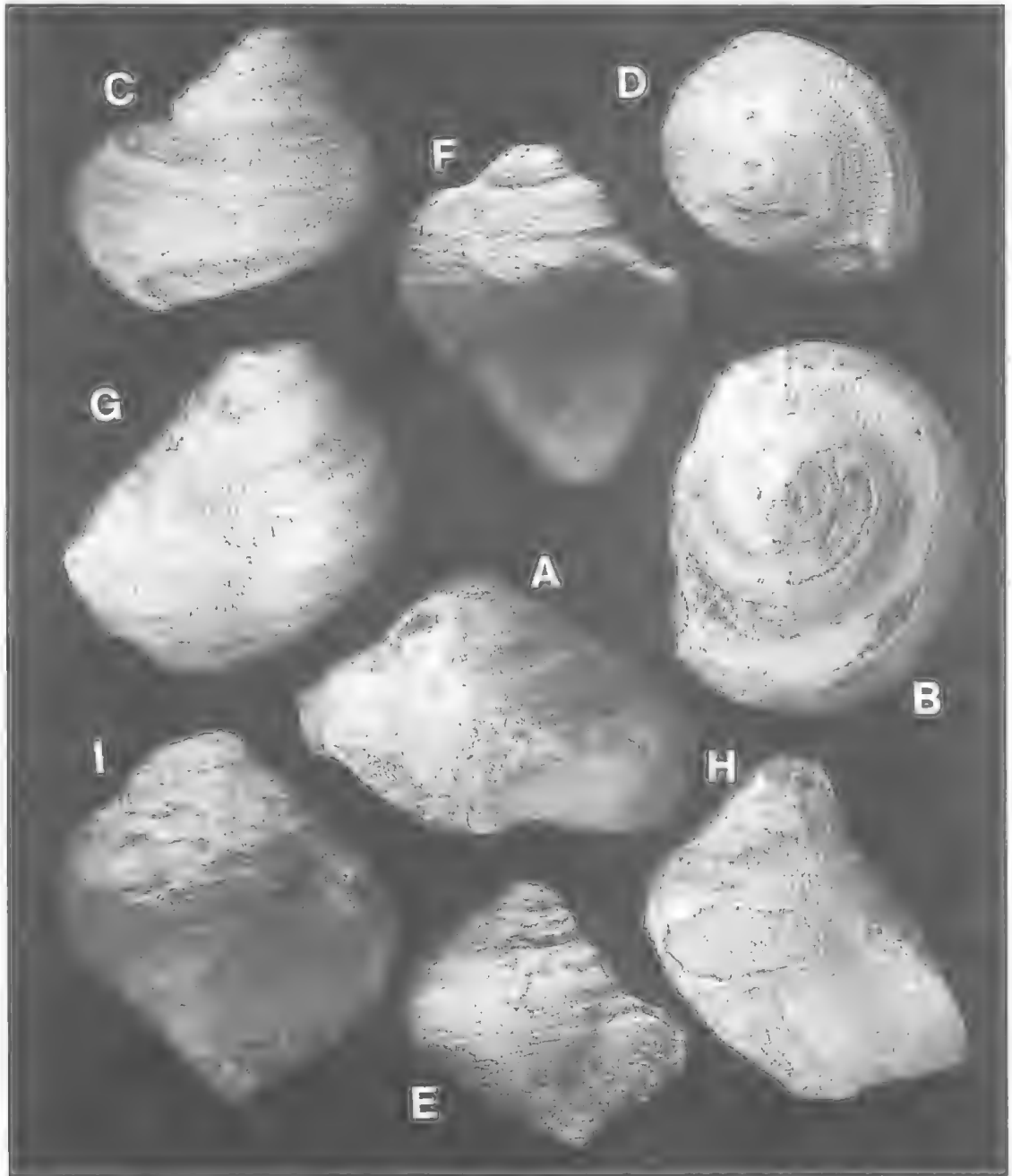


FIG. 5. *Brokenriveria pharlapensis* sp. nov. A, B, Holotype QMF32234, x 3. A, apertural view; B, apical view. C-E, paratype, QMF32268, x 2.8. C, side view. D, apical view. E, apertural view. F, QMF32273, x 2.8, apertural view. G, H, Paratype QMF32272, x 2.7. G, side view; H, apertural view. I, paratype QMF32274, apertural view x 2.8.

major thread which has 2 minor threads between it and the suture. Growth lines of 2 orders; numerous, fine, prosocline, slightly coarser growth lines intersect with spiral cords to produce nodes. Ap-

erture rounded, outer lip not preserved, inner lip thickened, and in some specimens reflected slightly. Shell relatively thickened for size. Protoconch unknown.

TABLE 3. Measurements for *Brokenriveria pharlapensis* sp. nov.

Specimen	height (mm)	width(mm)	approx. apical angle (°)
QMF32234	11.7	14.6	70
QMF32237	12.7	11.2	70
QMF32239	12.7	14.0	70
QMF32272	13.8	14.3	70
QMF32296	14.0	13.5	65
QMF33625	12.4	12.5	75
QMF33629	16.0	13.5	65
QMF33628	15.2	13.2	75
QMF33636	13.1	10.0	65

REMARKS. This species differs from *Gemininodosa langi* sp. nov. by its lack of very large nodes on the shell periphery. The specimen of indeterminate platyceratoid described below has a more rounded whorl profile, greater expansion rate and less prominent spiral ornament.

ETYMOLOGY. For 'Pharlap' Crossing of the Broken River.

#### *Gemininodosa* gen. nov.

TYPE SPECIES. *Gemininodosa langi* sp. nov. from the Middle Devonian Papilio Mudstone, Broken River Province, north Queensland.

DIAGNOSIS. Small to medium-sized, turbiniform, minutely phaneromphalus, with numerous spiral cords; upper whorl surface bears 2 spiral rows of large rounded nodes.

REMARKS. The lack of a sinus or selenizone, dominance of spiral ornament and the turbiniform shape indicates placement within the Holopeidae Wenz. Superficially the genus is like *Oriostoma* Munier-Chalmas but does not possess the wide umbilicus. The distinct nodose ornament renders the genus unlike any other members of the family but is reminiscent of the node- (and selenizone-) bearing Pleurotomariitoidea, such as *Nodonema* Linsley, 1968 and *Glyptomaria* Knight, 1945.

ETYMOLOGY. For the twin nodes adorning the shell.

#### *Gemininodosa langi* gen. et. sp. nov. (Fig. 6A-I)

MATERIAL EXAMINED. HOLOTYPE: QMF33611 from QML1092, Papilio Mudstone, Givetian, Broken River Province. PARATYPES: QMF33608-33610, QMF33612-33618, from QML1092, QML33638-33644 from QML1090.

DIAGNOSIS. As for genus.

DESCRIPTION. Medium-sized, turbiniform, minutely phaneromphalus, up to 16mm wide and 16mm high (Table 4) with an average spire angle of 75-115°. Sutures impressed, whorls embrace at midwhorl. Whorl profile overall rounded, flattened adjacent to the suture, rounded at midwhorl and lower whorl surface. Midwhorl dominated by 2 rows of large nodes, one at the edge of the flattened upper whorl surface the other near the periphery. A third less distinct set of nodes occurs below the midwhorl. Whorl surfaces are ornamented with many spiral cords, with at least 5 major cords on the lower whorl surface, 4 on the mid whorl, and 3 on the upper whorl surface. Growth lines fine, numerous and opisthocline; continuing across the midwhorl undeflected by any selenizone. Protoconch unknown.

REMARKS. This species differs from *Brokenriveria pharlapensis* and the indeterminate platyceratoid described below by possessing the twin row of nodes on the upper surface. The grossly similar *Nodonema granulatum* Linsley from the Middle Devonian Anderdon Limestone, is much smaller (holotype 6mm high), and possesses a distinct selenizone. *Kitikamispira ukalundensis* Cook, 1995, from the Emsian Ukalunda Beds of Queensland, and *Kitikamispira kanekoi* Kase & Nishida, 1988 from the Eifelian, Nakazato Formation, Japan both have nodes on all the spiral cords, and these spiral cords are strong and of equal intensity.

ETYMOLOGY. For Simon Lang.

#### Family PLATYCERATIDAE Hall, 1859 *Platyceras* Conrad, 1840

#### *Platyceras* (*Platyceras*) Conrad, 1840

TYPE SPECIES. *Pileopsis vetusta*, from the Lower Carboniferous of Queens County, Ireland by subsequent designation of Tate (1869).

#### *Platyceras* (*Platyceras*) sp. (Fig. 4E-G)

MATERIAL EXAMINED. QMF32641, from SD43e.

DESCRIPTION. Small, horn-shaped rapidly expanding shell, 5.1mm high, 11.5mm maximum width; first whorl in contact, second disjunct; whorl profile ovate, aperture broken, but basal lip deflected strongly downwards near apertural

margin. Ornament consists of fine, faint collabral growth lines and diffuse coarser growth rugae.

**REMARKS.** Substantial variation in members of the subgenus render it unwise to nominate a species on the basis of a single specimen. *Platyceras* (*P.*) sp. A. of Tassell (1982) from the Early Devonian of Taemas has more disjunct whorls whereas the Broken River specimen has the first whorl in contact. *Platyceras* (*P.*) *mansfieldense* Tassell, 1977 from the Early Devonian Loyola Limestone has similar ornament and has the first whorl in contact, but is a significantly larger form

**PLATYCERATOIDEA** gen. et sp. indet.  
(Fig. 6J,K)

**MATERIAL EXAMINED.** QMF34224 from QML1092.

**DESCRIPTION.** Turbiniiform, medium-sized, 13mm high and 13mm wide, average spire angle approximately  $110^\circ$ . Sutures impressed, with whorls embracing slightly above midwhorl. Whorl profile rounded. Ornament consists of numerous spiral cords of equal strength, and fine weaker, slightly prosocline collabral growth lines.

**REMARKS.** The single distinct specimen lacks the two orders of spiral threads characteristic of *Brokenriveria pharlupensis* and does not bear the twin cords of *Gemininodosa langi*. The turbiniform, shape, lack of sinus and simple ornament places the specimen in the superfamily, and it is possibly a platyceratid, but further assignment is impossible without a wider selection of material.

Superfamily and Family indet.  
**Burdikinia** Knight, 1937

**Burdikinia burdekinensis** (Etheridge, 1917)  
(Fig. 2E,F)

*Polyamma burdekeninesis* 1917 Etheridge: 16; Pl. 3 figs 1,2.

*Burdikinia burdekinensis* (Etheridge) Knight 1937: 711 (Etheridge) Knight 1941: 63; Pl. 57, figs 3a-h; Heidecker, 1959: 5, Pl. 2, fig. 2, Pl. 3, fig. 3a,b; Knight et al. 1960: 1309; fig. 205, 4a,b.

**MATERIAL EXAMINED.** QMF33578, QMF33579 from QML1083.

**DESCRIPTION.** Large, low-trochiform shell up to 35mm high, 55mm wide; apical angle of  $130^\circ$ . Suture channelled with keel on abaxial margin, whorls embrace on upper whorl face. Upper

**TABLE 4.** Measurements for *Gemininodosa langi* gen. et sp. nov.

Specimen	Height (mm)	Width (mm)	approx. apical angle ( $^\circ$ )
QMF33611	14.2	11.0	75
QMF33608	14.6	16.4	115
QMF3363E	16.3	13.9	98
QMF33641	14.1	14.1	90
QMF33642	13.5	10.3	135 (crushed)
QMF33644	12.2	10.9	90

whorl surface sloping and slightly concave, lower whorl surface rounded. Peripheral angulation at slightly above midwhorl. Aperture subrectangular. Base rounded, heavily abraded, with poorly preserved prosocline growth lines. Relicts of nodes preserved on periphery and on sutural keel.

**REMARKS.** The material is heavily abraded, lacking the basal ornament characteristic of the taxon, but it is otherwise indistinguishable from the holotype, and other material collected from the Burdekin Subprovince. A review of the higher taxonomy of this distinct gastropod is needed.

Superfamily MURCHISONIOIDEA  
Koken, 1896

Family MURCHISONIIDAE Koken, 1896  
**Murchisonia** D'Archaic & De Verneuil, 1841  
**Murchisonia** (Murchisonia)

**Murchisonia** (Murchisonia) *wandovalensis*  
sp. nov. (Fig. 7A-G)

**MATERIAL EXAMINED.** HOLOTYPE: QMF33680 from QML1092, Papilio Mudstone, Givetian, Broken River Province. PARATYPES: QMF33675-QMF33679, QMF33681-QMF33685, QMF34129 QMF34184, QMF34195-QMF34202 from L1092.

**DESCRIPTION.** Small, high-spined, turbiniform gastropod, up to 11mm high and 11mm wide (Table 5), with an apical angle of c.  $55^\circ$ . Suture impressed. Whorl profile angular with wide, mid-whorl, peripherally placed selenizone bordered by prominent 2 spiral cords. Upper whorl face steep, slightly concave. Lower whorl face rounded, bearing a spiral cord 1/3 below the selenizone. Whorls embrace at this lowermost cord, just below the mid-whorl. Growth lines fine, numerous, collabral; concave in the selenizone; somewhat sinusoidal between the lower bordering cord of the selenizone and the spiral cord on the lower whorl face. Base rounded aperture subrounded with slit at midwhorl.

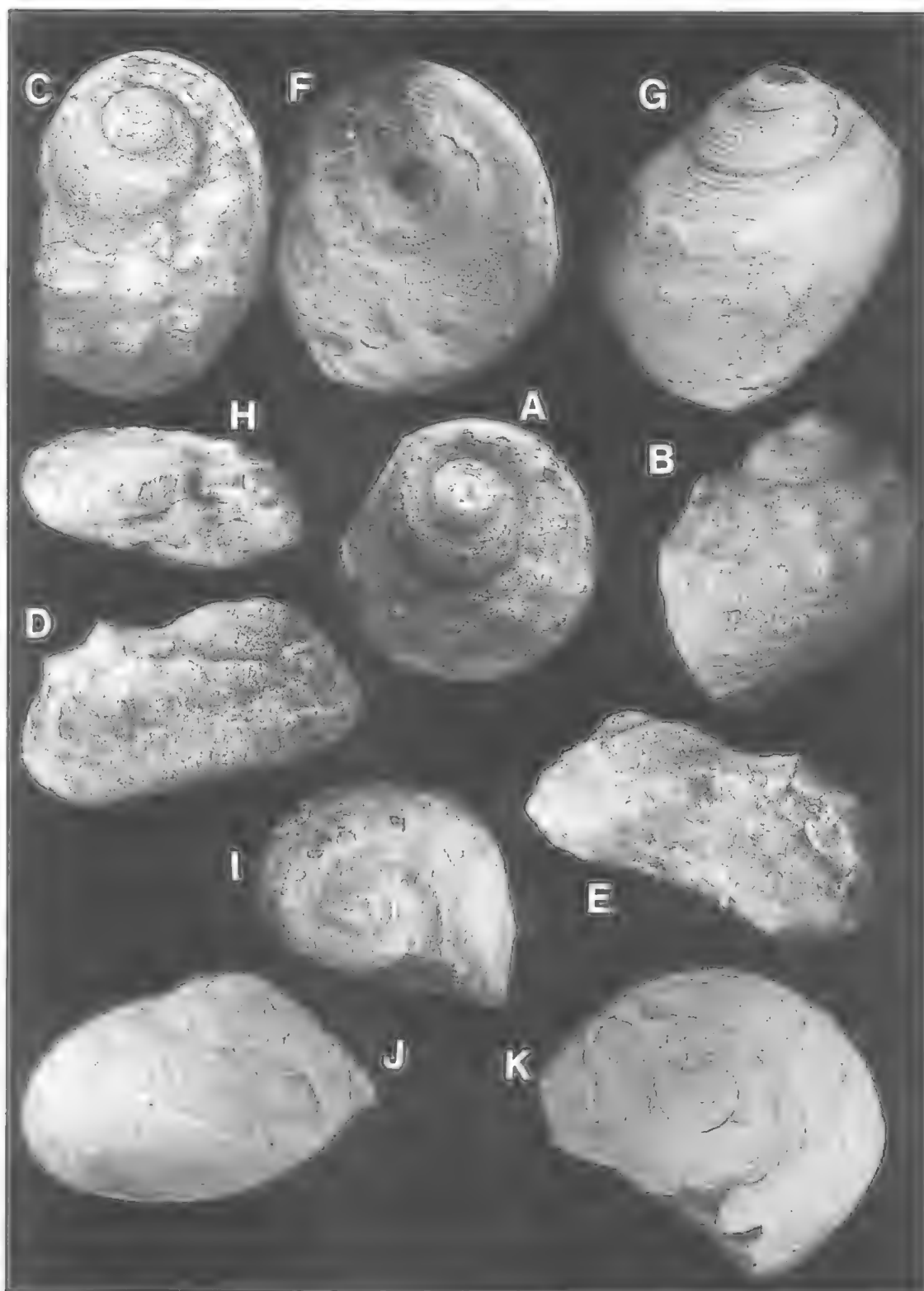




TABLE 5. Measurements for *Murchisonia* (*Murchisonia*)

Specimen	Height (mm)	Width (mm)
QMF33676	8.6	7.2
QMF33680	10.7	7.7
QMF33685	8.2	6.8
QMF34202	8.9	8.9

**DIAGNOSIS.** Small, somewhat turbiniform *Murchisonia* (*Murchisonia*), with additional spiral cord on lower whorl face, just below selenizone.

**REMARKS.** The material is similar to *M. (M.) fermioni* Tassell 1982 from the Early Devonian *Receptaculites* Limestone, New South Wales, however *M. (M.) fermioni* has a more impressed suture and lacks the spiral cord on the lower whorl face. From other species of the subgenus it differs in the less high-spired form, and generally, the presence of the lower whorl face cord.

**ETYMOLOGY.** For Wandovale Station.

***Murchisonia* (*Murchisonia*) *lawlessi* sp. nov.**  
(Fig. 8 A-I)

**MATERIAL EXAMINED.** HOLOTYPE: QMF33704 from QML1019, uppermost Dosey Limestone, Givettian, Broken River Province. PARATYPES: QMF33089, QMF34258, QMF33096, QMF33345, QMF33347, QMF33393, QMF33700, QMF34263 from QML1019.

**DIAGNOSIS.** Medium-sized, high-spired member of subgenus, with ridge on upper and lower whorl faces, more prominent on upper, but not defining a distinct cord.

**DESCRIPTION.** Medium-sized, high-spired an-omphalus gastropod, up to 18.4mm high, 12.0mm wide at base (Table 6) with an apical angle of approximately 22-30°. Whorl profile angular with peripheral selenizone bordered by two cords. Upper whorl face shallowly sloping with a low, rounded, spiral ridge, just below the suture. Suture impressed, whorls embrace well below midwhorl at lower spiral ridge. Selenizone narrow, located at midwhorl. Lower whorl face rounded and convex, with weaker ridge, slightly lower and wider. Base rounded, aperture rounded with slit at peripheral margin.

TABLE 6. Measurements for *Murchisonia* (*Murchisonia*) *lawlessi* sp. nov.

Specimen	Height (mm)	Width (mm)	approx. apical angle (°)
QMF33704	18.4	12.0	22
QMF33347	15.3*	7.6	22
QMF33700	16.5	11.0	25
QMF33345	17.6	9.4	30

**REMARKS.** The species is differentiated from other *Murchisonia* (*Murchisonia*) in the area by the ridge on the upper and lower whorl faces in addition to those bordering the selenizone.

*Murchisonia* (*Murchisonia*) *turris* de Koninck from the Early Devonian *Receptaculites* Limestone, New South Wales lacks the two additional ridges and is more high-spired. *Murchisonia* (*Murchisonia*) *anderdoniae* Linsley 1968, from the Middle Devonian Anderdon Limestone, North America, has a similar whorl profile and spire architecture, but is much smaller and lacks the upper and lower spiral ridges of *M. (M.) lawlessi*.

The material is superficially resemblant of *Ulrichospira kanekoi* Kase & Nishida from the Eifelian Nakazato Formation, Kitikami Mountains, Japan, but members of *Ulrichospira* have the selenizone high on the whorl, rather than midwhorl in this taxon.

**ETYMOLOGY.** For Phil Lawless.

***Murchisonia* (*Murchisonia*) sp. cf.**  
***M. (M.) fermioni* Tassell, 1982**  
(Fig. 7H,I)

**MATERIAL EXAMINED.** QMF33701, QMF34266, QMF33264 from QML1019.

**DESCRIPTION.** Small to medium-sized, turbiniform shell, up to 16.1mm high, 10.6mm wide, with a pleural angle of 35°. Whorl profile acutely angular, upper whorl face steep, lower flattened. Periphery at midwhorl bearing narrow selenizone bordered by 2 spiral threads. Suture impressed, whorls embrace slightly below selenizone. Base rounded. Aperture unknown. Growth lines fine, numerous, collabral, slightly opisthocline.

**REMARKS.** This species is separated from *M. (M.) wandovalensis* by the lack of spiral or-

FIG. 6. A-I, *Gemininodosa langi* gen. et. sp. nov. A,B. Holotype QMF33611, x 3.3. A, apical view; B, side view. C-E, Paratype QMF33642, x 3.7. C, oblique apical view; D, side view; E, apertural view. F,G, Paratype QMF33638, x 3.4. F, apical view; G, Side view. H,I. Paratype QMF32182 (crushed specimen), x 4. H, apertural view; I, apical view. J,K, *Platyceratoidea* gen. et sp. indet. QMF34224, x 3.7. J, Side view; K, apertural view.

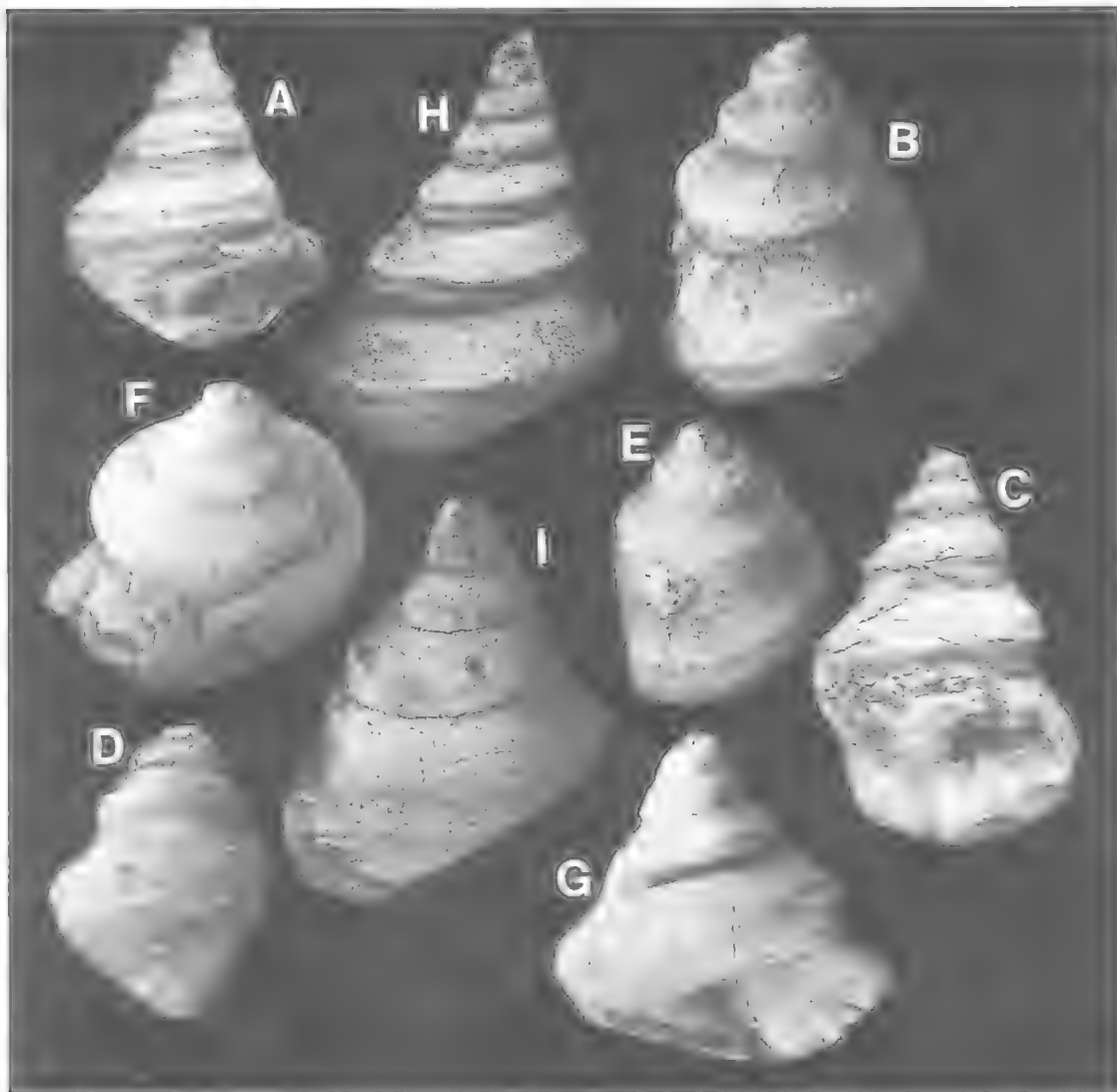


FIG. 7. A-G, *Murchisonia (Murchisonia) wandovalensis* sp. nov. A, Paratype QMF33676, apertural view x 5. B, C, Holotype QMF33680, x 4.7. B, side view; C, apertural view. D, E, Paratype QMF33685, x 4.5. D, apertural view; E, oblique side view. F, G, Paratype QMF34202 x 4.5. F, oblique side view; G, apertural view. H, I, *Murchisonia (Murchisonia)* sp. cf. *M. (M.) fermioni* Tassell, 1982. H, latex mould of QMF33701, x 3, side view. I, latex mould of QMF34266, x 3.5, side view.

nament additional to that bordering the selenizone and the more angular whorl profile. *Murchisonia (M.)* sp. is a higher-spired shell. The species is resemblant of *M. (M.) fermioni* Tassell, 1982 from the Early Devonian *Receptaculites* Limestone, New South Wales, but Tassell's taxon is slightly smaller, for this reason we tentatively refer the limited material to that taxon.

***Murchisonia (Murchisonia)* sp.**  
(Fig. 8J)

MATERIAL EXAMINED. QMF33686 from QML1019.

DESCRIPTION. Medium-sized, many-whorled, high-spired slender shell, 22mm height, 8mm basal width, with an apical angle 20°. Suture impressed with fine, weak, spiral ridges on the adjacent whorl surfaces. Whorl profile angular with peripheral,

midwhorl, concave selenizone bordered by prominent spiral cords of equal strength. Upper whorl surface begins flattened, thence is gently concave to periphery. Lower whorl face weakly concave. Base unknown. Growth lines unknown. Inner whorl surface rounded in cross-section, but aperture unknown.

REMARKS. The specimen closely resembles *Murchisonia* (*Murchisonia*) *akidota* Linsley 1968, from the Middle Devonian Anderdon Limestone, North America, but Linsley's taxon is much smaller, and has a more prominent spiral ridge on the lower suture, rather than weak lines above and below. Similarly *Murchisonia* (*Coelocaulis*) *procera* Oehlert 1888 from the Early Devonian of Saint-Germain-le-Fouilloux, France and *Murchisonia* (*Murchisonia*) *sculpta* (Perner, 1907) from the Late Silurian of Bohemia are larger and lack the ridges adjacent to the suture.

murchisoniid indet.  
(Fig. 4A,B)

MATERIAL EXAMINED. QMF33097, QMF33100, QMF34259 from QML1019.

DESCRIPTION. Medium-sized, moderately high-spined, turbiniiform gradate shell up to 28mm high and 20mm wide, with an apical angle of c. 30°. Upper whorl surface with prominent sutural ramp sloping very gently to peripheral rounded keel. Midwhorl surface wide and vertical, with selenizone bordered by 2 weak threads. Lower whorl face rounded, but poorly known in the material. Suture slightly impressed, situated at lower part of midwhorl surface. Base unknown. Collabral growth lines, fine, numerous, closely spaced, prosocline on sutural ramp and above selenizone, opisthocline below selenizone.

TABLE 7. Measurements for *Australoxa tasselli* gen. et sp. nov.

Specimen	Height (mm)	Width(mm)	approx. apical angle (°)
QMF33586	18.0*	8.6	20
QMF33587	18.0*	9.2	22
QMF33588	14.8*	6.5	19
QMF33589	16.9*	10.0	23
QMF33590	21.0*	11.5	25
QMF33708	16.8*	7.2	20
QMF33712	12.0*	5.7	20

REMARKS. Blodgett (pers. comm.) has examined photographs of this material and suggests that the Broken River specimens are congeneric with a new species of murchisoniid from north America. There is not enough material to confidently erect a genus or species.

Order CAENOGASTROPODA Cox, 1959  
Superfamily LOXONEMATOIDEA  
Koken, 1889  
Family LOXONEMATIDAE Koken, 1889  
*Stylonema* Perner, 1907

*Stylonema*? sp.  
(Fig. 10A)

MATERIAL EXAMINED. QMF33102 from QML1019.

DESCRIPTION. High-spined; many-whorled; small gastropod, 6.9 mm high; 1.4mm wide; apical angle sharp; approximately 12°; sutures grooved; sutural slope high; whorl profile rounded; aperture unknown; growth lines and sinus unknown.

REMARKS. Poor preservation and lack of material prevents assignment to species. The whorl profile and grooved sutures suggest reference to *Stylonema* but definite assignment awaits further material.

#### *Australoxa* gen. nov.

TYPE SPECIES. *Australoxa tasselli* sp. nov.

DIAGNOSIS. Medium-sized, high-spined; angular whorl profile; growth ornament of prominent opisthocline ribs. Angular periphery bears shallow but sharp sinus. Lower whorl profile with spiral cord.

REMARKS. The coarse ribbing suggests affinities to Palaeozygopleuridae, but the shallow sinus suggests placement within the Loxonematidae. The angular whorl profile is grossly suggestive of *Donaldiella*, but the growth parameters are significantly different for that genus as indicated by the differing growth lines. We place the genus in the Loxonematidae, but the genus appears intermediate between the two families and is derived from a time of great change in both.

ETYMOLOGY. Latin, Austral, southern, loxa, implying loxonematid affinities.

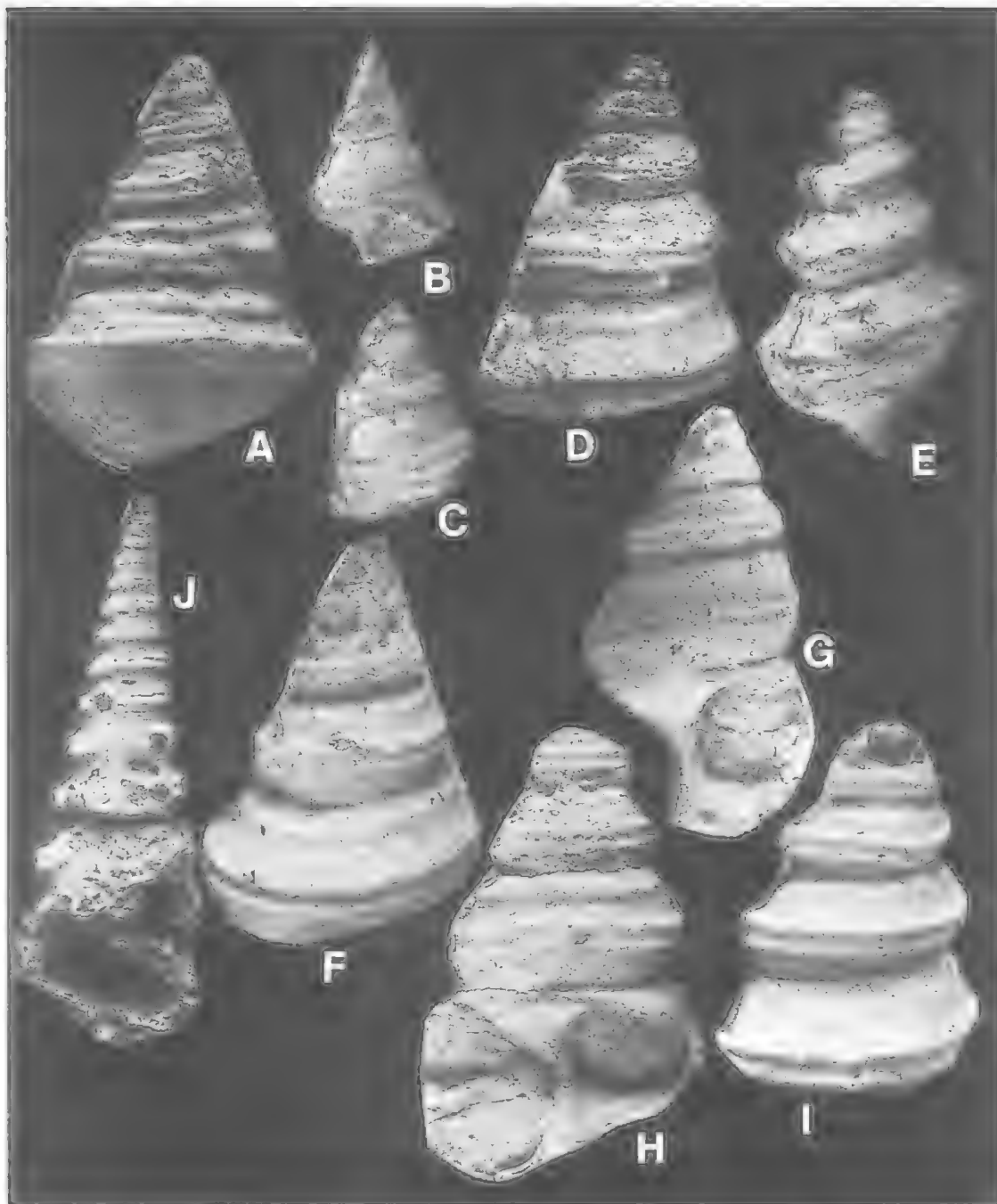


FIG. 8. A-I, *Murchisonia (Murchisonia) lawlessi* sp. nov. A, latex mould of holotype QMF33704, x 3.1, side view. B, latex mould of paratype QMF33092, apertural view x 4. C, latex mould of paratype QMF33095, x 3.5. D, latex mould of paratype QMF34260, side view x 3.6. E, latex mould of paratype QMF34258, x 3.5, side view. F, latex mould of paratype QMF33700, x 3.5, side view. G, latex mould of paratype QMF33096, x 3.6, apertural view. H, latex mould of paratype QMF33089, apertural view, x 4 last whorl abraded. I, latex mould of paratype QMF33707, x 4, side view. J, *Murchisonia (Murchisonia)* sp. QMF33686, x 3.5.

TABLE 8. Measurements for *Palaeozygopleura dodgeyi* sp. nov.

Specimen	Height (mm)	Width (mm)	approx. apical angle (°)
QMF33605	19.0	7.6	22
QMF33606	15.1	6.8	20
QMF33607	17.2	8.3	~20

***Australoxa tasselli* sp. nov.**  
(Fig. 9E-L)

**MATERIAL EXAMINED.** HOLOTYPE: QMF33586, from QML1092, Papilio Mudstone, Givetian, Broken River Province. PARATYPE: QMF33587-QMF33603, QMF33708-QMF33711, from QML1092.

**DIAGNOSIS.** As for genus.

**DESCRIPTION.** Medium-sized, high-spired, anomphalous, up to slightly more than 22mm high, 12mm basal width, with a pleural angle of 19-25° (Table 7). Up to 7 whorls present in the material, but in general the apical whorls are missing. Whorl profile angular, with periphery slightly below midwhorl. Lower whorl face convex. Upper whorl face slightly convex to nearly flat with numerous strong opisthocline ribs which continue to the lower whorl face, only deflected at the periphery. Sinus expressed as a shallow, but sharp U-shaped deflection of the ribs on the peripheral angulation. A weaker spiral cord is present on the lower whorl face. Suture impressed; whorls embrace just below lowermost spiral cord. Base of holotype has subdued ribbing, otherwise, base rounded. Finer collabral growth lines preserved. Aperture unknown, but growth lines suggest it is rounded with a sharp, shallow invagination in the outer lip. Protoconch unknown.

**REMARKS.** This abundant taxon has the characteristic ribbing and angular whorl profile separating it from other loxonematids. There is superficial similarity to *Loxonema magnificum* Spitz, 1907 and *L. ingens* Frech from the Lower Devonian of the Carnic Alps. Both species are much larger. *L. ingens* lacks the angulation, having nodes instead and has finer ribbing. *L. magnificum*, whilst poorly preserved, shows relicts of nodes rather than a sinus-bearing angulation. Another superficially resemblant taxon is *Trochus? lamellosus* Lindstrom, 1884 from the Silurian of Gotland, but that taxon has a different whorl profile, a flattened base and is clearly not a loxonematid.

**ETYMOLOGY.** For Chris Tassell.

Loxonematidae indet.

**MATERIAL EXAMINED.** QMF32062 from QML541.

**DESCRIPTION.** Poorly preserved, large, many-whorled, high-spired shell, 35mm long, approximately 15mm wide at with an apical angle of c. 5-101°. Sutures impressed, sutural slope moderately high, approximately 15°. Coarse ribs suggested in the specimen, other external shell features not preserved.

**REMARKS.** Overall shape, sutural slope and impression suggests affinity to the Loxonematidae Koken. The specimen resembles *Loxonema angelicum* d'Orbigny of de Koninck (1877: pl. 4, fig. 9), from the Early Devonian of New South Wales but is too poorly preserved for reliable comparison.

Family PALAEOZYGOPLEURIDAE

Horny, 1955

***Palaeozygopleura* Horny, 1955**

***Palaeozygopleura dodgeyi* sp. nov.**

(Fig. 9B-D)

**MATERIAL EXAMINED.** HOLOTYPE: QMF33604 from QML1092. PARATYPES: QMF33605-33607 from QML1092. QMF33620 from QML1090.

**DIAGNOSIS.** Small to medium-sized member of the genus, with thick opisthocyrt ribs.

**DESCRIPTION.** Small to medium-sized, high-spired gastropod which grew to slightly more than 19mm high and 7-9mm wide, with an apical angle of approximately 20° (Table 8). Base rounded, anomphalus; sutures impressed, whorl profile rounded with surface bearing numerous, thick, opisthocyrt ribs which extend from suture to suture, with a slight subsutural shelf on the uppermost whorl face. Finer collabral lines are present between rugae on QMF33620, not preserved on other specimens. Aperture not preserved, whorl profile and growth lines suggest that this was rounded, with broad sinus.

**REMARKS.** The species is smaller than, and lacks the change in rib spacing of *L. alticostatum* Tassell 1982 from the Early Devonian of New South Wales. *L. australis* (Cresswell) of Tassell (1978) is also similar, but has finer, more numerous ribs. The type species *P. alinae* (Perner) from the Lower Devonian of the Prague Basin, has finer ribbing, and is significantly smaller. This

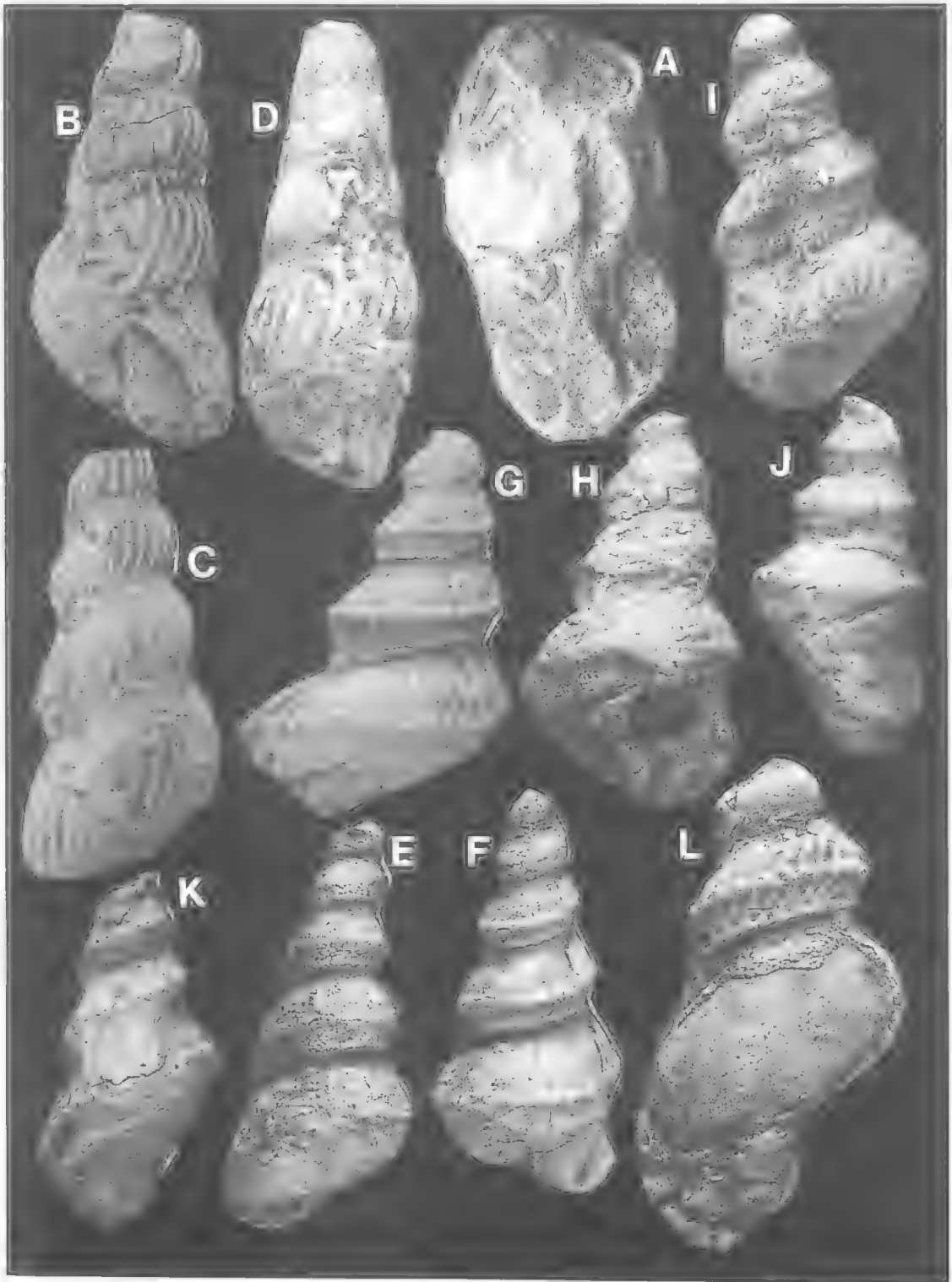


TABLE 9. Measurements for *Leptogyma queenslandicus* sp. nov.

Specimen	Height (mm)	Width (mm)
QMF33673	7.7	5.7
QMF33674	7.5	6.4
QMF34204	6.0	6.6
QMF34209	5.9	4.9
QMF34213	6.3	5.7

species lacks the protoconch but is at the upper range of size diagnosed for the genus by Horny (1955). Both *P. sibleyense* Linsley and *P. joanni* Linsley from the Middle Devonian Anderdon Limestone of North America, are smaller, *P. joanni* has finer ribbing, *P. muoni* Tassell, 1982 from the *Receptaculites* Limestone of New South Wales lacks the prominent ribbing, and is smaller.

ETYMOLOGY. For Paul 'Dodgey' Tierney and Scott 'Dodgey' Hocknull.

Family PSEUDOZYGOPLURIDAE  
Knight, 1930

PSEUDOZYGOPLURIDAE gen. et sp. indet.  
(Fig. 9A)

MATERIAL EXAMINED. QMF33584 from QML1089.

DESCRIPTION. The specimen is 2 whorls of a large, high-spined anomphalus shell. Basal width is 21.7mm, with the height of the 2 whorls 26.4mm. Whorl profile rounded; periphery slightly below midwhorl with the whorl surface dominated by thick, widely-spaced, slightly sigmoidal ribs. Suture impressed, embracing whorl slightly below periphery. Base somewhat conical. Preparation of specimen revealed no preserved fine growth lines. Shell moderately thick.

REMARKS. Given the large size and the prominent ribbing, the specimen belongs to the family, but cannot be further indentified. *Laxonema altacostatum* Tassell 1982 from the *Receptaculites* Limestone of New South Wales is similar, but its ribs are less sigmoidal.

Superfamily SUBULITOIDEA Lindstrom, 1884  
Family SUBULITIDAE Lindstrom, 1884  
Subfamily SOLENISCINAE Wenz, 1938

*Soleniscus* Bayle

TYPE SPECIES. *Soleniscus typicus* Meek & Worthen, 1861.

*Soleniscus* sp. cf. *Soleniscus subcostata*  
Schlotheim (Fig. 10 E,F)

MATERIAL EXAMINED. QMF33692-QMF33694 from QML1019.

DESCRIPTION. Medium sized, fusiform, up to 25mm high, 16mm wide, with an apical angle of c. 35°. Suture slightly impressed; whorls embrace slightly below midwhorl. Whorl profile rounded, periphery slightly above midwhorl. Surface ornamented by numerous sinusoidal growth lines. Aperture and base unknown.

REMARKS. *Macrochilina* Bayle was placed in synonymy with *Soleniscus* Meek & Worthen by Knight et al. (1960) but forms ascribed to that genus have a generally squatter form than those given to *Soleniscus*. A strikingly similar, but much larger form is *Macrochilina arcuata* Schlotheim of Mansuy (1912) from the Givetian of Yunnan. *Macrochilina subcostata* Schlotheim of Whidborne (1892) is of similar size and ornamentation and the Broken River material is referred to that taxon. Following Knight et al. (1960) both these taxa should be accommodated within *Soleniscus*. Perhaps separation of elongate and squat forms of the genus can be accommodated in 2 subgenera *Soleniscus* (*Soleniscus*) Meek & Worthen, and *Soleniscus* (*Macrochilina*) Bayle.

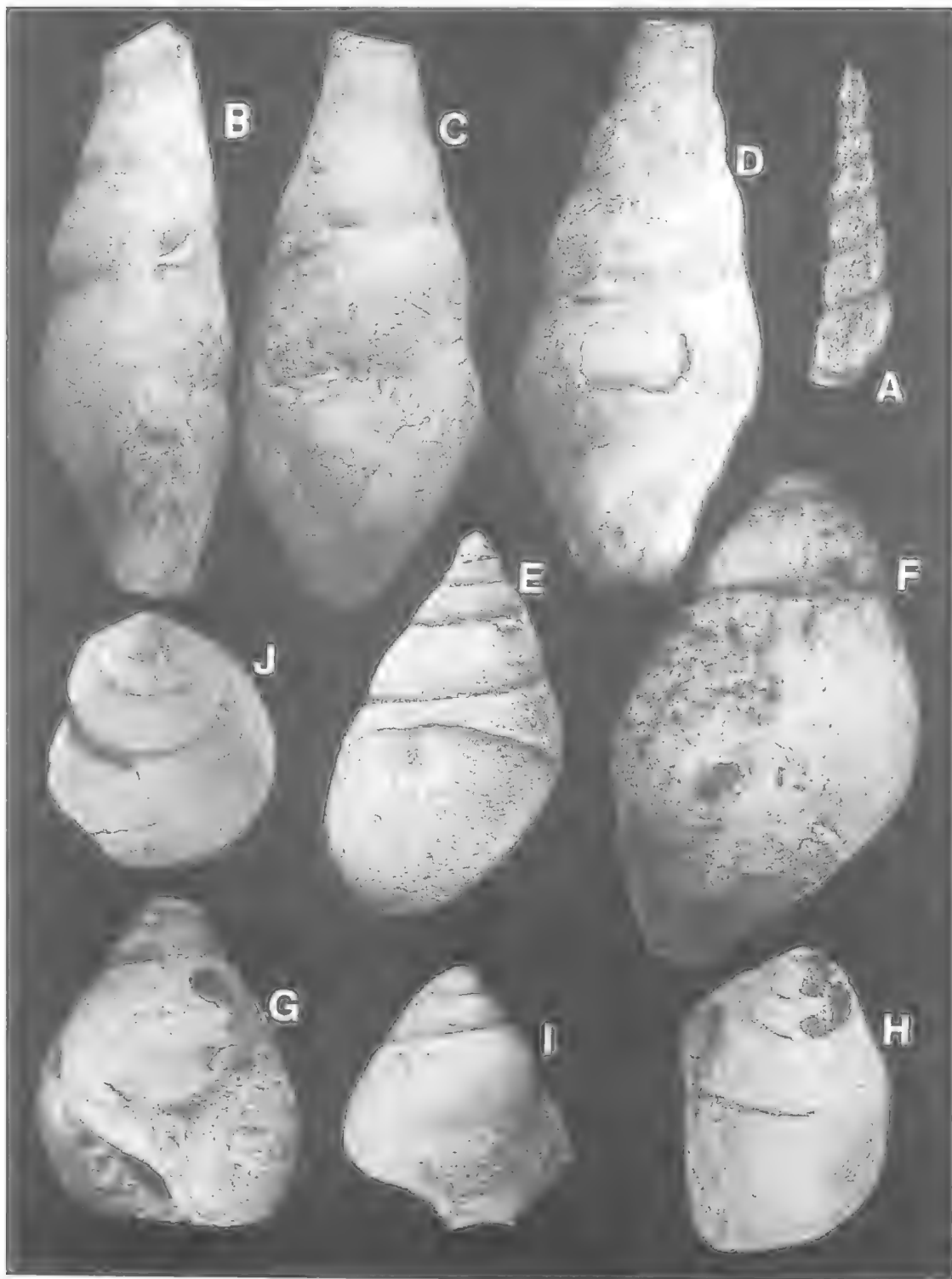
*Leptogyma queenslandicus* sp. nov.  
(Fig. 10G-J)

MATERIAL EXAMINED. HOLOTYPE: QMF33673, from QML1092, Papilio Mudstone, Givetian, Broken River Province. PARATYPES: QMF33674, QMF34203-QMF34213 all from QML1092.

DIAGNOSIS. Small, turbiniform, *Leptogyma* with very fine growth lines and weak wide sinus.

FIG. 9 A, palaeozygopleurid indet. QMF33584, apertural view x 2.2. B-D, *Palaeozygopleura dodgeyi* sp. nov. B, C, Holotype QMF33608 x 3.5. B, apertural view; C, side view. D, Paratype QMF33607 side view x 3.5. E-L, *Australovata tasselli* gen. et sp. nov. E, F, Holotype QMF33586 x 3.3. E, side view; F, apertural view. G, Paratype QMF33589 x 3.5 side view. H-J, Paratype QMF33708, x 3.6. H, apertural view. I, side view. J, side view. K, Paratype QMF33588, x 3.5, side view. L, Paratype QMF33590, x 3.1, side view.





**DESCRIPTION.** Small, turbiniform gastropod, up to 7.7mm high and 6.6mm wide (Table 9), apical angle c. 25°. Sutures slightly impressed, whorls join at periphery. Final whorl very large in proportion to earlier part of conch. Protoconch unknown. Whorl profile rounded, periphery below midwhorl, upper whorl face occupies 2/3 of profile. Growth lines very fine, numerous, closely spaced with a weak wide sinus. Base rounded. Columellar lip thickened, probable minor fold.

**REMARKS.** *Leptogyma* Knight, 1936 is separated from *Auriptogyma* Perner, 1903 by the thinner, unfolded columella in the latter. Thickening on the columellar lip confirms the generic identification. *Leptogyma australis* Tassell 1982, from the Early Devonian of New South Wales is higher spired than the Broken River material.

**ETYMOLOGY.** For the state of Queensland.

Family CODONOCHEILIDAE Miller, 1889  
*Mitchellia* de Koninck, 1876

**TYPE SPECIES.** *M. striatula* de Koninck, 1876, from the limestone of the Yass District, New South Wales, by original designation

**DIAGNOSIS.** See de Koninck 1877, or the 1898 translation.

**DISTRIBUTION.** Early Devonian (Emsian). *Receptaculites* Limestone, Taemas, New South Wales. The destroyed holotype specimen was from black argillaceous limestone from the Yass District, New South Wales and is most probably Early Devonian; Middle Devonian (Givetian) Papilio Formation, Broken River Province, north Queensland.

**REMARKS.** Knight et al. (1960) regarded *Mitchellia* as a junior synonym of *Scoliostrongylus* Braun, but as pointed out by Tassell (1982) the gerontic growth stage of the aperture is twisted downwards and, not upwards and is more constricted where it joins the main spire.

*Mitchellia striatula* de Koninck, 1877  
(Fig. 10, B-D)

**MATERIAL EXAMINED.** QMF32643 from SD21.

**DESCRIPTION.** Medium-sized, high-spired, dextrally-coiled shell; early whorls not present in this specimen which is 38mm high and has 15mm maximum width. Apical angle is approximately 20°. Sutures moderately impressed; sutural slope approximately 15°. Whorl profile rounded, and rounded base. Aperture broken but, laterally constricted at final growth stage to an elongate oval shape. Ornament consists of more than 12 spiral threads. At final growth stage the threads are deflected downwards, indicating deflection of apertural growth.

**REMARKS.** The aperture is incomplete, broken at the point of deflection, but it is clearly constricted and the spiral threads show a marked downward deflection, identical to the more complete but smaller silicified specimens described by Tassell (1982). The specimen is at least double the size of those recorded by de Koninck (1876) and Tassell (1982), but is retained in the species due to the morphological equivalence.

#### ACKNOWLEDGEMENTS

We thank Peter Jell for his encouragement and assistance throughout this project. We thank John Jell and John Talent for providing material from their collections. Phil Lawless, Scott Hoeknull, Paul Tierney, Colin McHenry, Donna Case and Reints Lootsma are thanked for field assistance. Robert Blodgett and Chris Tassell are thanked for their helpful comments on the manuscript.

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FIG. 10. A. *Stylonematal* sp. latex mould of QMF33102 x 7. B-D, *Mitchellia striatula* (de Koninck, 1876) QMF32643 x 2. B, apertural view; C-D, side views. E, F, *Soleniscus* sp. cf. *Soleniscus subcostata* Schlotheim. E, Latex mould of QMF33692 x 2. F, latex mould of QMF33693 x 3. G-J, *Leptogyma queenslandiens* sp. nov. G, H. Holotype QMF33673. G, apertural view x 6.3. H, oblique view x 6.3. I, J. Paratype QMF33213 x 6.3. I, apertural view. J, oblique view.

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**PTYCTODONT JAW FROM THE BROKEN RIVER PROVINCE, NEQ.** *Memoirs of the Queensland Museum*. 42(1): 80. 1997: - A single ptyctodont gnathal recovered from the Papilio Mudstone (Middle Devonian, Givetian), Broken River Province, north Queensland, represents the first macrofossil evidence for the family in the Middle Devonian of Australia whilst both Early and Late Devonian ptyctodontids are known (Long, 1991). Possible ptyctodontid microfossils have been described from Emsian and Givetian units in the Broken River Province by De Pomeroy (1994). The new specimen is a gnathal with a well preserved tritoral surface. The specimen was recovered from QML1018, SW of Storm Dam, Wando Vale, where outcrops of the Papilio Mudstone form part of an extensive muddy carbonate platform succession whose sedimentology has been detailed by Lang et al. (1993). Jell et al. (1993) place the Papilio Mudstone at Storm Dam within the *varcus* to *hermanni-cristatus* Conodont Zone.

### Systematic Palaeontology

Order PTYCTODONTIDA Gross 1932

Family PTYCTODONTIDAE Woodward 1891

*Ptyctodus* Pander 1858

?*Ptyctodus* sp.

(Fig. 1)

1996 ?ptyctodontid indet., De Pomeroy: 431, fig. 6b, ?O,P

**Material.** QMF35438, from QML1018, SW Storm Dam, Broken River Province, NQ. Papilio Mudstone, Middle Devonian, Givetian. Collected A. Cook & N. Camilleri.

**Description.** Right? superognathal 44mm long; functional edges steep and narrow with a short anterior cutting edge. External surface relatively smooth with faint curving lineation. Large depression on the internal surface. Gnathal widens posteriorly to double width at about two-thirds along its length (from 4mm to 8mm across); dental plate with smoothly concave, sharp biting edge. Tritor 3mm wide, 17mm long with approximately 5 tritoral dentine plates per millimetre.

**Remarks.** Ptyctodonts were predominantly marine bottom feeders with a small gape, bordered with a series of few strong beak-like dental plates (Denison, 1978). Ptyctodontid gnathalia do not consist of bone but are pure dentine. Well worn dental surfaces of this specimen appear to be preserved as vivianite. Ptyctodont toothplates are commonly found as isolated elements in the Middle and early Upper Devonian of North America and Europe. In the last century many were given specific names but cladistic analysis of the late twentieth century has revised and suppressed many of these taxa. Detailed study of such toothplates may prove them to be useful biostratigraphic tools.

### Acknowledgments

We thank E.D. McKenzie for assistance with preparation.

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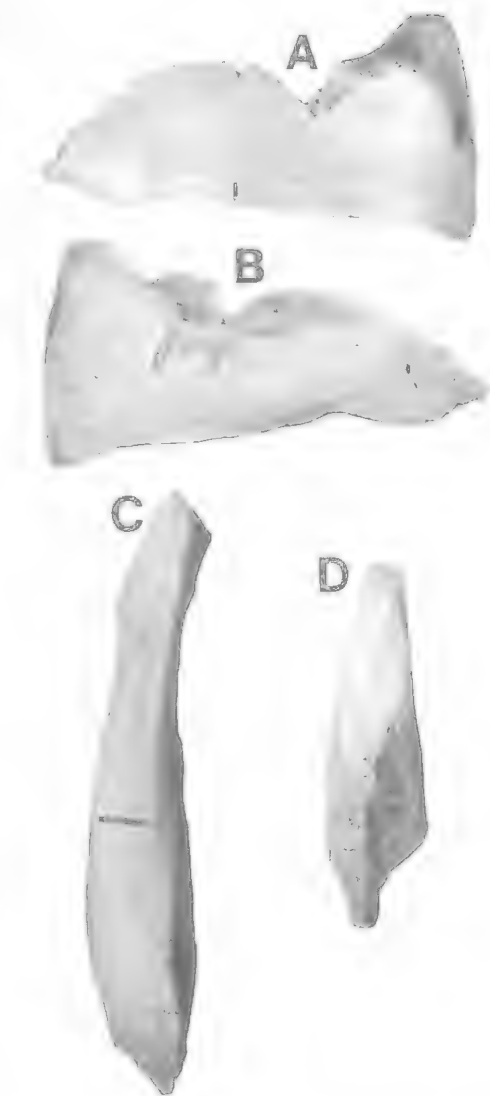


FIG. 1. ?*Ptyctodus* sp., x 1.2. A, external (labial) view. B, internal (lingual) view. C, occlusal view. D, anterior view.

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Susan Turner & Alex G. Cook, Queensland Museum PO Box 3300 South Brisbane QLD 4101 Australia; 20 December 1996.

## SYMBIOTIC STROMATOPOROID-NAUTILOID ASSOCIATION, MIDDLE DEVONIAN, NORTH QUEENSLAND

ALEX G. COOK AND MARY WADE

Cook, A.G. & Wade, M. 1997 06 30: Symbiotic stromatoporoid-nautiloid association, Middle Devonian, north Queensland. *Memoirs of the Queensland Museum* 42(1): 81-89. Brisbane. ISSN 0079-8835.

The stromatoporoid *Clathrocoilon* *spissa* encrusts specimens of *Diademoceras* obtained from the Middle Devonian (Givetian) Papilio Mudstone, Broken River Province and Burdekin Formation, Burdekin Subprovince, north Queensland. Stromatoporoid growth commenced and flourished while nautiloids were in an upright living position. *Diademoceras*, here described for the first time in Australia, is considered upright benthonic to barely nekto-benthonic. □ *Nautilida*, *Devonian*, *stromatoporoid*, *symbiosis*, *Queensland*.

Alex G. Cook & Mary Wade, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 10 March 1997.

Devonian nautiloids from northeastern Australia are poorly known, despite the seminal works of Teichert (1940) and Teichert & Glenister (1952). Large and diverse faunas occur in the Burdekin Basin (Jell, pers. comm.) but are less diverse in the adjacent Broken River Province.

Five fragmentary specimens of *Diademoceras* were recovered from WSW of Storm Dam, (QML1017 and BRJ62), from the Papilio Mudstone, Broken River Province, north Queensland. Three specimens were recovered from the Burdekin Formation, Golden Valley area, near Fanning River, Burdekin Subprovince, NQ. This is the first description of *Diademoceras* from eastern Australia. *Clathrocoilon* *spissa* is a widespread encrusting stromatoporoid (Cook, 1994). Specimens from Papilio Mudstone were weathered from lime-mudstone units interpreted as having been deposited on a shallow-water, open marine, muddy shelf (Lang et al., 1993). The Papilio Mudstone contains an abundant fauna including corals, brachiopods, stromatoporoids and conodonts, indicative of a Givetian age (Jell et al., 1993). Material from the Burdekin Formation was retrieved from carbonate mudstone and packstone units, interpreted by Cook (1995) as representing deposition on a shallow to moderately deep (5-60m) carbonate shelf within the geographically restricted Burdekin Basin. The Burdekin Formation also contains a diverse assemblage of corals, stromatoporoids, brachiopods and molluscs. Sparse conodont faunas (Talent & Mawson, 1994) also indicate a Givetian age.

### STROMATOPOROID OVERGROWTHS

Five of the eight *Diademoceras* specimens possess a sheath of encrusting stromatoporoid, two others have partial encrustation and the remaining specimen has been abraded. Cut specimens show attached corals (several aulopodid and rugose corals), but growth of these was dominated by that of the stromatoporoid associates. Polished blocks and thin sections were prepared to reveal growth detail of the encrusters. The stromatoporoid was identified as *Clathrocoilon* *spissa* (Lecompte, 1951). Each sheath consists of many growth phases of *C. spissa*, punctuated by growth inhibition and termination surfaces (*sensu* Kazmierczak, 1971). Growth was thickest on the ventral margin of the nautiloid, thinner inside its open coil. Many growth phases completely enveloped the shell indicating that development of some phases was uninhibited by the nautiloid's resting position on the substrate. These must have grown while this part of the shell was raised above the substrate. Other growth was more spasmodic. Crescentic nodes on the shell flanks of *Diademoceras* developed at the aperture. They are likely to have protected siphons for the usual paired inhalent water currents during pauses in growth but became overgrown after the shell grew further (Fig. 4c.) Thus we conclude that at times the nautiloid positioned itself upright and stromatoporoid growth commenced during the life of the nautiloid. The nautiloid, encumbered with such stromatoporoid encrustation, would have hardly been capable of significant motion in the water column, as observed by Wade (1988) who mistook poorly preserved encrusting stromatoporoid growth for part of a thick shell wall. The availability to epizoans supports the

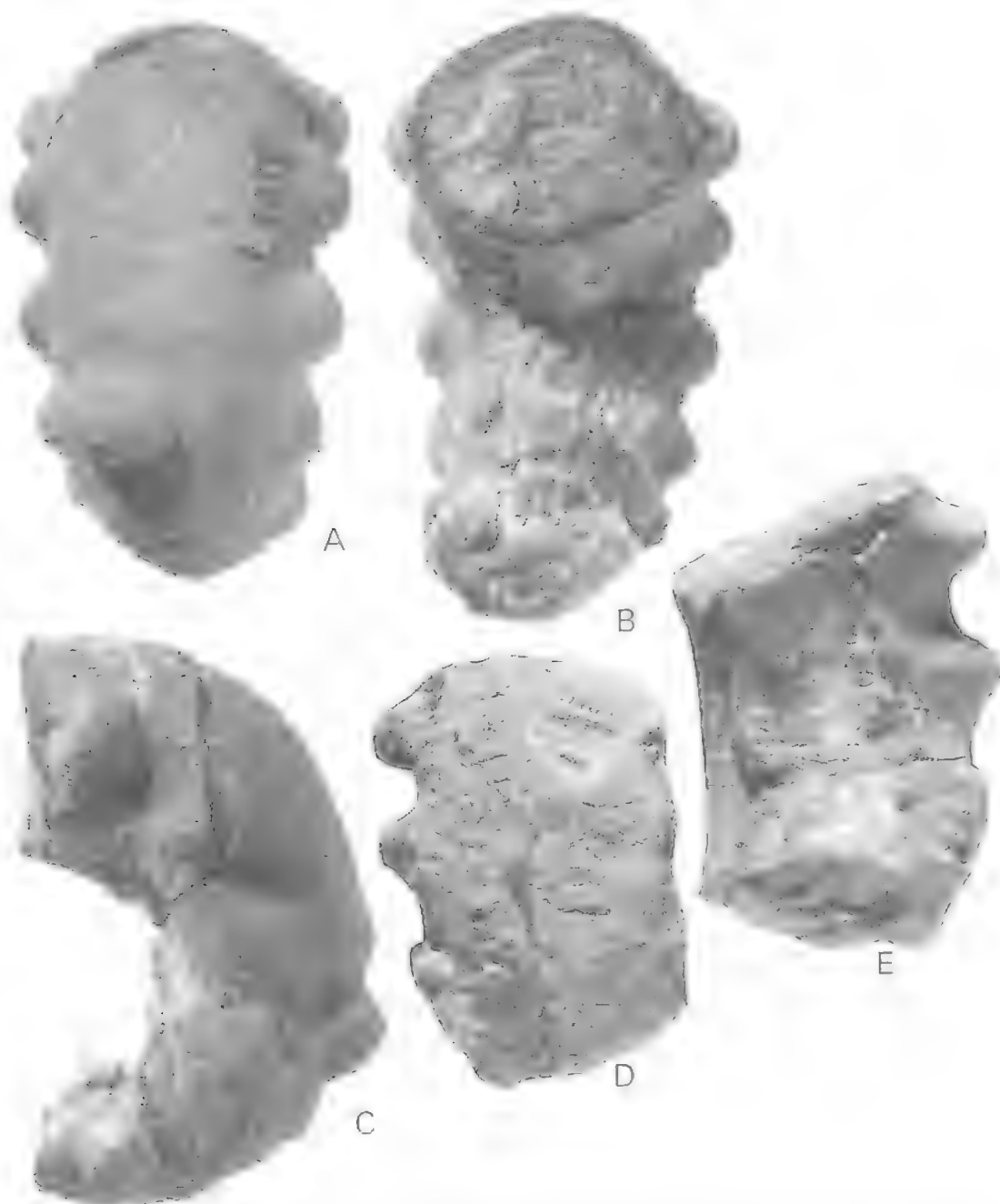


FIG. 1. *Diademoceras submammillatum* (Whiteaves) x 0.5. A-C, QMF32218, prior to sectioning. A, dorsal view; B, ventral view; C, side view. D, E, QMF33877. D, dorsal view; E, ventral view.

suggestion that the form was benthonic or barely nektobenthonic. Observed growth interruptions would have occurred through limited partial burial, shell rotation with growth or some other

benthic adjustments. Some growth interruptions may be due to changes in sea-floor sedimentation effecting the vitality of the stromatoporoid. Furnish & Glenister (1964) have suggested that all



Nautilida were nektobenthonic and posthumous floaters. Considering the mass of encrusting stromatoporoid, it is unlikely that significant post mortem transport occurred here, except some by wave action.

Encrustation upon nautiloids has been reported by Teichert (1964) who stated that '*irrespective of normal bouyancy requirements such shells could not have floated appreciably after the animal died*' (Teichert, 1964: K125). Frey (1988) recorded bryozoan encrustation upon *Treptoceras duseri*, a michelinoceratid from the Ordovician of Ohio. These bryozoan sheaths were uniformly thin, and Frey (1988) concluded that whilst *Treptoceras duseri* was nektonic, he could not determine whether encrustation took place during the life of the nautiloid.

#### SYSTEMATIC PALEONTOLOGY

Phylum PORIFERA Grant

Subphylum STROMATOPOROIDEA

Nicholson & Murie

Order STROMATOPORELLIDA Stearn

Family STROMATOPORELLIDAE Lecompte

*Clathrocoilona* Lecompte 1951

#### *Clathrocoilona spissa* (Lecompte) 1951

REMARKS. Cook (1994) has described *C. spissa* from the neighbouring Burdekin Subprovince and noted its presence within Givetian strata of the Broken River Province. The material here is adequate for identification, displaying the characteristic irregular architecture, occluded irregular galleries in both tangential and vertical section, and tripartite laminae.

Phylum MOLLUSCA

Class CEPHALOPODA

Subclass NAUTILOIDEA Agassiz

Order RUTOCERATIDA Flower & Kummel

REMARKS. Nautilida are often characterised by their thin siphuncular walls, in which layering is difficult to detect (Flower, 1964), although all Nautiloidea may be observed or inferred to have had two layers applied to a basal membrane which is rarely seen in fossils (Wade, 1988). Siphuncles in the *Diademoceras* material described here are clearly layered, consisting of two thick layers and possibly one thin layer (see below).

#### Family RUTOCERATIDAE Hyatt, 1884

REMARKS. Most workers post-dating Flower & Kummel (1950) have agreed that Rutoceratidae, or an inclusive larger taxon, is intermediate between Oncocerida and Nautilida (Kummel, 1964). Although Teichert (1967, 1988) changed his view of the taxonomic status of Rutoceratidae as the basal family to the basal suborder of Nautilida, Flower (1964; 1988) persisted in recognising Rutoceratida between Oncocerida and Nautilida, with Rutoceratidae as the basal and nominate family. *Diademoceras*, which Flower (1949) assigned to the Rutoceratidae, has open coiling and a nodose shell, respectively rare and almost unheard of in the Oncocerida. These are rather commonplace in Nautilida. They occur here with a thick outer (supportive) layer in the connecting rings, and thin inner (osmotic pump) layer. Turek & Marek (1986) have found oncocerid muscle scars in *Ptenoceras*, assigned to Rutoceratidae, order not stated. Rutoceratidae thus appear to be 'not yet' Nautilida. The material we have is inadequate for major taxonomic revision. Faced with the choice of withdrawing a mostly unseen and inadequately described Rutoceratina to the Oncocerida or accepting Flower's original evaluation of their status, we accept his placement.

#### *Diademoceras* Flower, 1945

*Diademoceras* Flower, 1945: 677; Flower 1949: 74; Kummel, 1964: 418; Zhuraleva, 1974: 124.

TYPE SPECIES. *Diademoceras palmeri* Flower, 1949, by original designation from the Middle Devonian (Givetian), Cherry Valley Limestone of New York.

REMARKS. Flower (1945) erected the genus, but did not describe or figure the type material. Flower (1949) fully diagnosed and described it. He further remarked that additional taxa of *Diademoceras* were found within the Manitoban Limestone, of which *D. submammatum* (Whiteaves) was the only described species. ?*Diademoceras ajense* Zhuraleva, 1974, from the Givetian of the southern Urals, is based on fragmentary material and is poorly known. *Diademoceras ventrolobatum* Lai & Zhang, 1988 from the Middle Devonian (Givetian) Qiziqao Formation is the most recently described member of the genus.

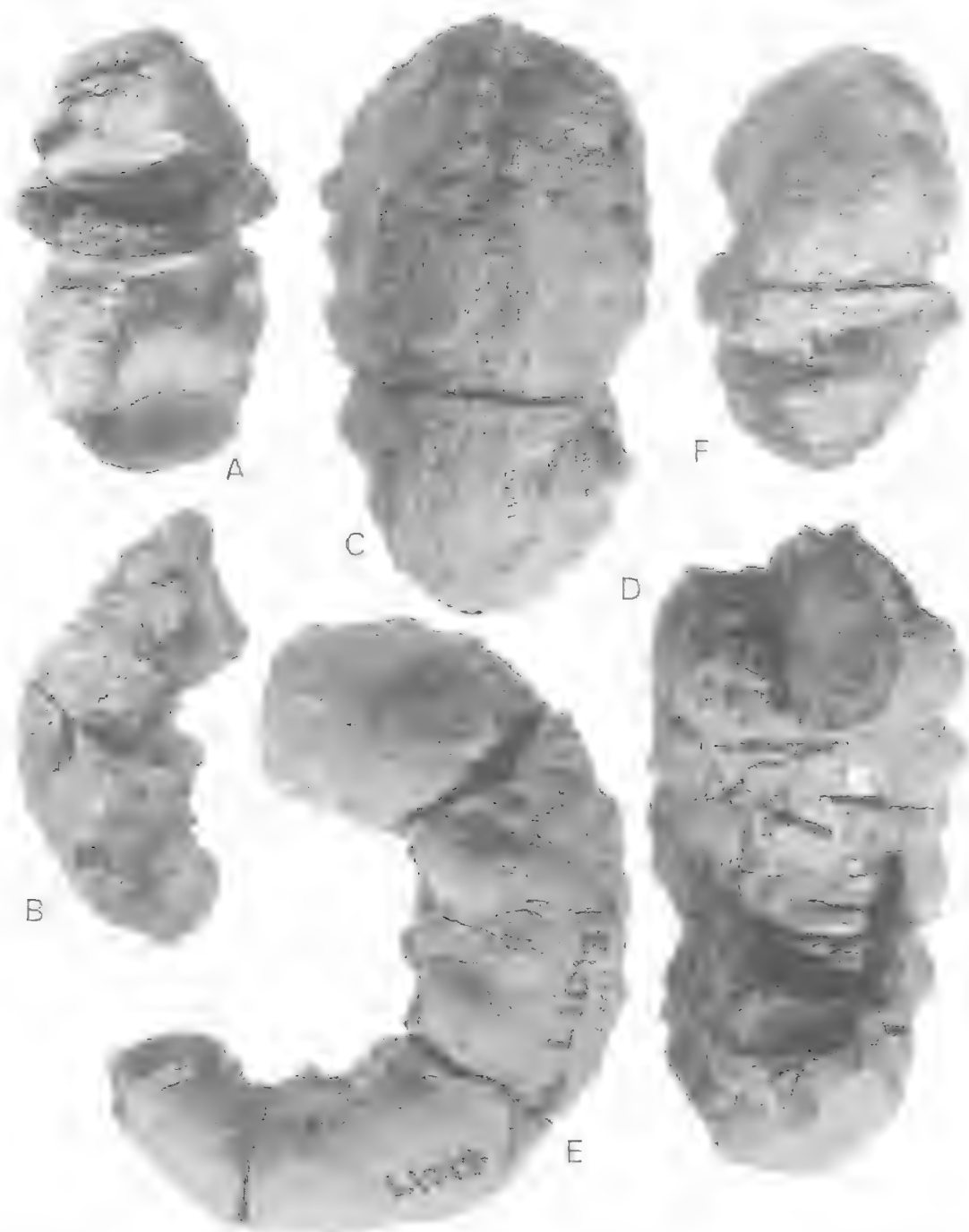


FIG. 2. *Diademoceras submammilatum* (Whiteaves) x 0.5. A,B,F, QMF32219, prior to sectioning. A, dorsal view; B, ventral view; F, side view. C-E, QMF32217. C, dorsal view; D, ventral view; E, side view.

***Diademoceras submamillatum***  
(Whiteaves, 1891) (Figs 1-4)

*Gyroceras submamillatum* Whiteaves 1891: 107, pl. 10, figs. 1a,b.

*Diademoceras submamillatum* (Whiteaves) Flower 1949: 75.

**MATERIAL EXAMINED.** QMF11896, collected J. Jell, from the Papilio Formation, SW of Storm Dam; QMF32212, QMF32217-9; from QML1018, collected N. Camilleri & A. Cook, 1 km S of Storm Dam, Papilio Formation, Broken River Province, north Queensland. QMF33877, QMF33879, QMF33880 collected D. Johnson & R. Henderson, from the Burdekin Formation, Golden Valley area, 'Fanning River' Station, NQ.

**PRESERVATION.** The nautiloid material is heavily recrystallised. Stylolites are common, and there is widespread loss of shell by solution. Septa in particular, may have been lost by aragonite solution because the calcite chamber fill is well preserved leaving adjacent crystallised chamber fills separated by thin spaces. Frequently septa are represented only by a thin, black, linear iron mineralisation. Since Allison (1988) established the sequence of early diagenetic minerals as francolite, iron sulfide, calcite, it is reasonable to trust shell-like shapes and positions of thin layers of iron mineralisation. In thin section these are represented by black lines which not only follow either surface of the septa, but may mimic septal or shell wall laminae when the original structure is lost by solution or recrystallisation. Here, as is common in open marine environments, phosphatisation was elided. Fibrous drusy calcite lined the chambers in both sectioned specimens, but this was sporadically replaced by coarsely crystalline calcite which filled the remainder of the cameral space.

Every thin section is deficient in shell material in some areas. All specimens were freed by surface weathering and have undergone some modern erosion and breakage. Some breakage presumably predates burial, since no whole whorls could be fitted together and body chambers are poorly preserved, but the original emptiness of some siphuncles and chambers is evidence against significant post-mortem movement on the sea floor although it was well above the fair weather wave base.

**DESCRIPTION.** Shell large, cyrtconic, up to 18 cm high and 9 cm wide (Table 1) representing up to a complete volution. Coiling was exogastric and open for there is no trace of dorsal contact on fragments of any diameter. Whorl broadly depressed, ovate in transverse section, with a height

TABLE 1. Morphometric data for *Diademoceras submamillatum* (Whiteaves) from the Papilio Mudstone and Burdekin Formation.

Specimen	height (mm)	W <sub>ant</sub> (mm)	W <sub>max</sub> (mm)	Volution (%)	Node spacing (mm)
QMF11896	150	45	75	130	21, 36, 34
QMF32212	164	40	60	225	N/A
QMF32217	182	42	90	250	22, 28, 31, 32, 32, 31, 34
QMF32218	160	48	63	195	17, 20, 29, 24, 33, 32
QMF32219	102	40	62	135	N/A
QMF33877	125	50	64	72	35, 37
QMF33879	125	-	-	230	-
QMF33880	129	34	65	70	26

to width ratio of 3:4. The smooth, broadly rounded arch of the venter and dorsum continues across the ventro- and dorsolateral areas to the rather narrowly rounded lateral areas (Figs 1-3). These are intermittently wholly taken up as the sites of large, anteriorly-facing flanged siphons, like those of *Ptenoceras*. As in *Ptenoceras* these are closed by subsequent growth which excluded detritus and thus formed so-called spines. Their detailed structure will be discussed below after shell walls. Posteriorly on the whorl the siphons are represented by small peaks instead of large spines, as previous descriptions have discussed. Dorsolaterally the walls are more depressed than ventrolaterally, they are almost flattened slopes, rather than curves, so that the dorsum can appear bluntly triangular overall. The siphuncle is near ventral, with constricted, dorsally sub-cyrtchoanitic necks which grade laterally into suborthochonanitic necks ventrally (Fig. 4B). The connecting rings are thick and obviously two-layered. Moderate expansion of the connecting ring within the chambers is consequent upon neck shape. A thick outer layer dorsally is developed from most of the tip of the swollen septal neck, but is more obscure in origin ventrally (Fig. 4B). This outer layer ends against the previous septum. A thin inner layer arises from the whole inner edge of the septal neck and adheres to the thick outer layer to its termination around the previous septal neck, thereafter the thin inner layer adheres to the constricted previous neck, and curved ad-posteriorly outward until it contacts the inner layer of the previous connecting ring. In this fashion the inner layers are connected to one another throughout the siphuncle's length, but the thick outer layers are localised to each chamber. Because of the curvature of the inner

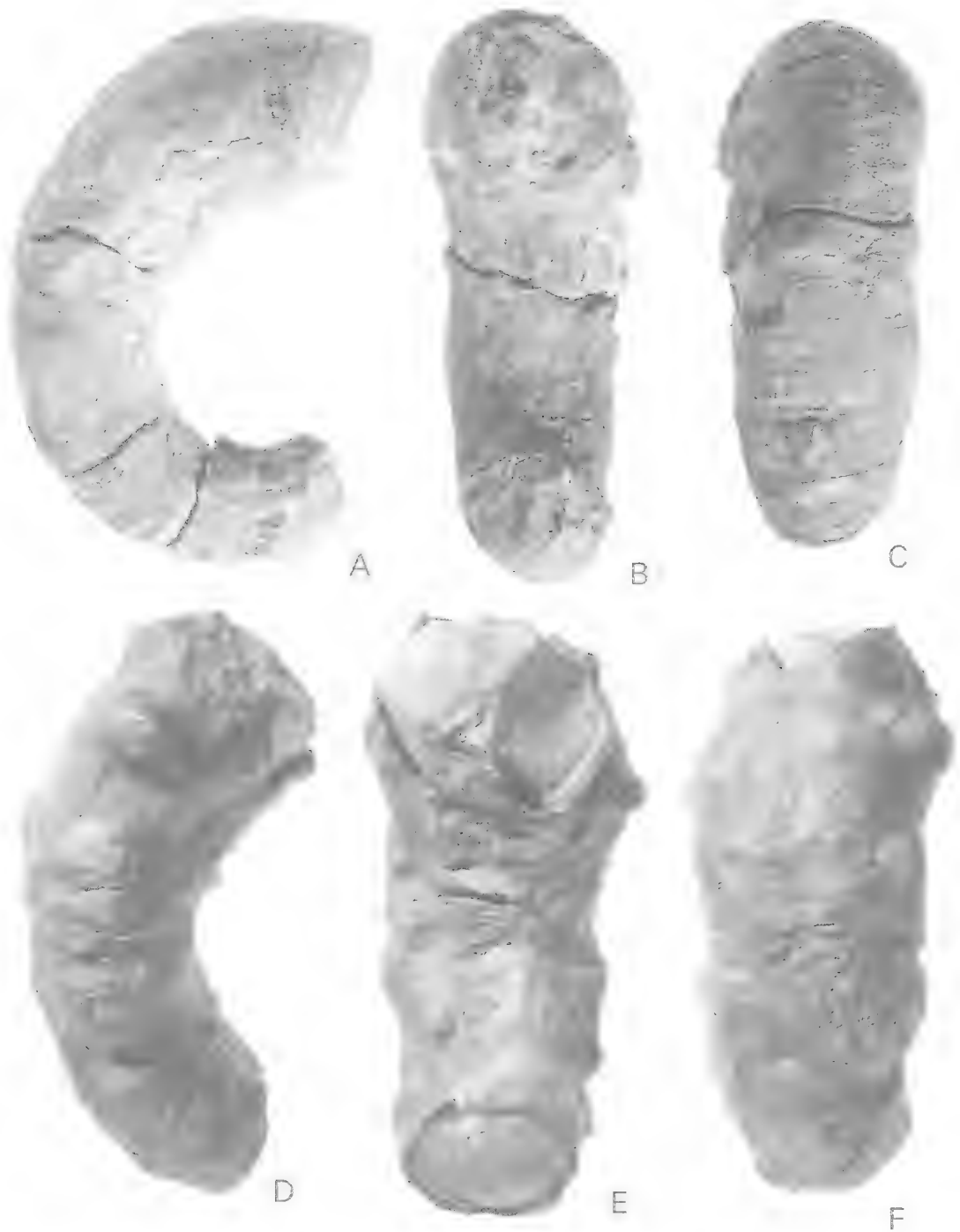


FIG. 3. *Diademoceras submammilatum* (Whiteaves) x 0.5. A-C, QMF 32212. A, side view; B, ventral view; C, dorsal view. D-F, replica of QMF 1896.

layer, it did not always match the previous neck (or stay matched after death), there is often a sediment-filled space between the bent dorsum of the previous neck and the inner layer of the con-

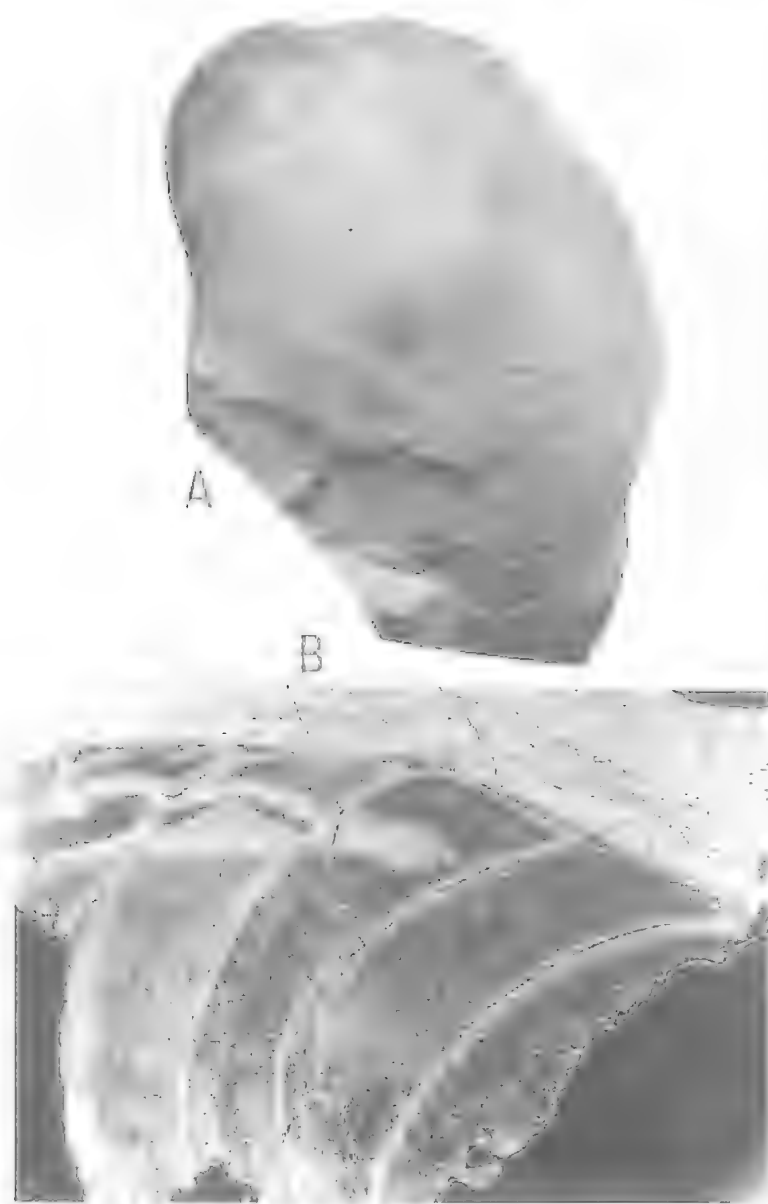


FIG. 4. *Diademoceras submamillatum* (Whiteaves), A, QMF33880, showing longitudinal ribs, faint growth lines and ventral sinus; B, Photo negative of QMF32218 slightly oblique through siphuncle, with encrusting *Clathrocoelona spissa* (Lecompte), x 1.9.

necting ring; this space appears in many longitudinal views of the siphuncle, and a similar space may appear more rarely ventrally.

The septa are swollen toward the dorsum of the neck and within it, but were otherwise thin. They are recrystallised wherever preserved. The septal flaps appear to have been long and relatively thick but are nowhere clearly seen. The shell wall

appears to be two-layered, sometimes separated by a dark line and otherwise by a gap. Poor preservation and abundance of stylolitisation within these structures does not allow us to determine with confidence whether this layering is primary or of diagenetic origin. It has the appearance of typical marine phreatic cement. The outer layer is coarsely prismatic, almost fibrous and not nearly as prone to recrystallisation as the inner layer. The inner layer is thinner in smaller cross-sections, but locally varied in thickness.

External ornament, as described by Flower (1949), is poorly known on most of the specimens as five of the eight specimens are completely sheathed in encrusting stromatoporoid. QMF33880 shows strong, narrow, longitudinal ribs on the shell surface, and they are slightly reflected on the internal mould (Fig. 4A). The ribs can be detected by changes of shell thickness, in cross-sections of other specimens and also on the internal moulds of some specimens. Suture with broad, slight ventral saddle, and broad ventrolateral lobes, with narrow saddle on the sharp umbilical angle; nearly straight across the dorsum. Growth lines of QMF33880 indicate a ventral sinus.

The shell possesses a row of short, rounded, thickly crescentic nodes oriented concave forward, relatively regularly spaced in any individual, up to 38mm apart. Sections indicate blocky calcite growth

within the spines indicating they were hollow.

**REMARKS.** Whiteaves (1891) described a poorly preserved taxon which is of similar size, possesses similarly spaced relicts of nodes and nearly straight sutures and hence is undifferentiable from the Broken River material. The type

species, *D. palmeri*, is a little smaller than Whiteaves' taxon, and has weak ventral lobes but may prove to be conspecific. *D. ventrolobatum* Lai & Zhang from the Middle Devonian of Guangxi, is significantly smaller. Wade (1988) misinterpreted the worn stromatoporoid encrusting QMF11896, the first specimen collected, interpreting this sheath as very thick layered original shell, because it faithfully reproduced the paired spines and shell outlines, and the stromatoporoid is very poorly preserved on that specimen.

If the outer wall lamina was not always present, forming symmetric lateral siphons and minor structures, and passing below every kind of epizoan, it could be suspected of being an epizoan too.

Separation of the hollow spines from the chamber by shell wall growth preceeding septa formation is observed, and validated by the shapes of exposed chamber fills which show the smooth, low rises under the nodes. Only the clean node-fills witness to front walls to the nodes, and the calcite growth, interpreted as phreatic growth, testifies to their shape as do the epizoan overgrowths. The smooth shell wall bases were perhaps added to the living chamber soon after the shell's siphons were closed, by reactivation of the mantle. All cephalopods repair by mantle reactivation, so this method is not unusual, and the gradual forward movement of the growing body would bring a smooth curve of body adjacent to the space within the closed siphon. This would allow a slight bulge, and account for the observed shape of the walls.

The undoubtedly aragonitic nautiloid shell recrystallised so completely, an explanation of the relatively good preservation of the microstructure of the stromatoporoid is required. Such differential preservation in these specimens would suggest that the original stromatoporoid mineralogy differed from that of the nautiloid, and by inference was probably calcitic. Stromatoporoids have been variously inferred as having skeletons which were calcitic (Galloway, 1957; Kershaw, 1990; Rush & Chafetz, 1991) or aragonitic (Stearn, 1975; Stearn & Mah, 1987). This material shows circumstantial evidence that the stromatoporoid was calcitic, but demonstrates no more than association of preserved calcite phases than Kershaw (1990).

#### ACKNOWLEDGEMENTS

We thank John and Peter Jell for encouragement and some material. We thank Bob Hender-

son for providing the Burdekin Formation material. The photography and library sections of the Queensland Museum are thanked for their generous assistance.

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**NEW INFORMATION ON THE NARROWLY-RESTRICTED SKINK, *NANGURA SPINOSA*.** *Memoirs of the Queensland Museum* 42(1): 90. 1997. Surveys of vertebrates of dry rainforests of south and mideastern Queensland during 1992 (Horsup et al., 1993) led to the discovery of the skink *Nangura spinosa* Covacevich, Couper & James, 1993. This is a distinctive, burrowing skink which was found in a 300m section of dry, gently-sloping creek bank in semi-evergreen vine thicket in Nangur State Forest (26°07'S 151°58'E), 20 km north of Murgon, SEQ. This was, until recently, the only known locality for *N. spinosa*.

On the 27 February, 1997 one of us (GA) observed a tail protruding from a burrow on a road embankment in Oakview State Forest, SEQ (26°07'23"S 152°19'01"E). An adult skink was removed from the burrow. It was photographed (QM transparencies NR 360 - NR 373) and released. While being handled, the specimen shed its tail. This has been registered in the Queensland Museum (QM162787), where our identification of the skink as *N. spinosa* was confirmed. Oakview S.F. is a new locality for *N. spinosa*. The collection site is approximately 40km east of Nangur S.F.

Additional searches along the road embankment for *N. spinosa* in Oakview S.F. on 28 February and 6 March, 1997 revealed 22 'active' burrows. Two further burrows were observed 7m and 27m up-slope from the road. Thirty-six specimens were seen: 23 adults, 1 sub-adult and 12 juveniles. Each burrow was occupied primarily by a single adult ( $n = 18$ ). One was occupied by 2 adults; one by 2 adults and 3 juveniles; three by 1 adult and 2 juveniles; and three by 1 adult and 1 juvenile. One adult, 1 sub-adult and 2 juvenile *N. spinosa* were weighed and their snout-vent (SVL) recorded. The adult measured 92.0mm SVL and weighed 26gm; the sub-adult measured 78.2 mm SVL and weighed 14.1 gm; juveniles suspected to be neonates (with umbilical scars) weighed 1.5gm (s.d. = 0,  $n = 2$ ) and had an average 37.8mm SVL (s.d. = 1.6,  $n = 2$ ).

The vegetation at all sites was Araucarian Notophyll Vine Forest (Horsup et al., 1993) on Quaternary alluvials, at an altitude of approx. 600m. Burrows in the road embankment (mean road embankment height = 106.9cm, s.d. = 26.6,  $n = 23$ ) were in three clusters along 1.4km of road and were set into the bank at an average height of 55.7cm (s.d. = 25.5,  $n = 23$ ) above the road. Burrow entrances were usually remote from ground cover ( $n = 15$ ), associated with rocks ( $n = 5$ ) or associated with tree bases or surface roots ( $n = 4$ ). The only exception was a burrow at the base of an old termite mound. Average size of burrow entrances was 8.1cm wide (s.d. = 3.3,  $n = 23$ ) and 4.9cm high (s.d. = 2.1,  $n = 23$ ). Each burrow had a smooth 'resting platform' near the entrance, with an average width of 11.1cm (s.d. = 4.7,  $n = 23$ ) and a length of 8.6cm (s.d. = 3.6,  $n = 23$ ). All had north-easterly aspects.

During daylight at Oakview S.F., we observed individuals either with tails visible at burrow entrances, heads slightly protruding from burrow entrances or on the resting platforms. One juvenile was observed approximately 15cm beyond a 'resting platform'. When approached, it retreated into the burrow. Nocturnal observations of road side burrows between 21:22 and 22:09hrs revealed 16 *N. spinosa* with tails visible at burrow entrances. The ambient temperature at this time was 21°C. Specimens of *N. spinosa* apparently 'rest' at burrow entrances from where they 'ambush' prey (Covacevich et al., 1993; Wilson, 1994). The presence of individuals at burrow entrances in Oakview S.F. may relate to either thermoregulatory or foraging behaviour.

Faecal samples of *N. spinosa* from Nangur S.F. contained a diverse range of arthropod remains (Covacevich et al., 1993). Locating visible evidence of faecal or feeding remains

at the Oakview site was hindered by heavy rains. A beetle carapace was the only possible prey remnant found close to a burrow.

Searches of road embankments in both similar and different soils and with similar aspects and vegetation in Oakview S.F. failed to reveal further evidence of *N. spinosa*. Much of the forest has been planted with Hoop Pine, *Araucaria cunninghamii*, leaving remnant strips of Araucarian Notophyll Vine Forest between plantation compartments. Larger remnants of NVF occur only on the steeper slopes where plantation establishment was not practical. The presence of two active burrows on slopes away from the road embankment shows that this species is not restricted to road embankments or the creek banks reported by Covacevich et al. (1993).

*N. spinosa* was a 'species known only from the type collection', and 'rare in Australia, but not currently considered endangered or vulnerable ...' (Covacevich et al., 1993). Under the Nature Conservation (Wildlife) Regulation 1994, this species was 'rare' in Queensland. With the discovery of this second population, the status of *N. spinosa* should be changed to that of a 'species with a very restricted distribution in Australia and with a maximum geographical distribution of less than 100km ...'. It remains 'a species ... rare in Australia ... not currently considered endangered or vulnerable ...' (Thomas & McDonald, 1989). Clearing of rainforest has ceased on Queensland state forests. However, dry rainforests have no legislative protection (Covacevich & McDonald, 1993). On freehold land they are still cleared and survive only as remnants. In state forests, vine thickets continue to suffer deleterious changes due to inappropriate fire regimes, disturbance by domestic stock and Hoop Pine logging. Further work is required to define the distribution of *N. spinosa* and to investigate relationships between supporting vegetation, soils and aspect. This information would be useful in refining the conservation status of *N. spinosa* and in devising management plans to conserve this species.

#### Acknowledgments

Thanks are due to Geoffrey Smith and Teresa Eyre for assistance with the preparation of this note. Funding for this work was provided through the Forest Wildlife Section's involvement in the Comprehensive Regional Assessment Vertebrate Fauna Survey program in Queensland. Jeanette Covacevich and Patrick Couper assisted us to prepare these data for publication.

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A NEW SPECIES OF *SALTUARIUS* (LACERTILIA: GEKKONIDAE) FROM  
GRANITE-BASED, OPEN FORESTS OF EASTERN AUSTRALIA

P.J. COUPER, C.J. SCHNEIDER AND J.A. COVACEVICH

Couper, P.J., Schneider, C.J. & Covacevich, J.A. 1997 06 30: A new species of *Saltuarius* (Lacertilia: Gekkonidae) from granite-based, open forests of eastern Australia. *Memoirs of the Queensland Museum* 42(1): 91-96. Brisbane. ISSN 0079-8835.

*Saltuarius wyberba* sp. nov., from the 'granite-belt' of southern Queensland and northern New South Wales, is separated from three of the four previously-known members of the genus in lacking male preanal pores. From the fourth, *S. swaini* (an obligate rainforest species), it is distinguished by smaller size, greater dorsoventral compression, shape and spinosity of the attenuated tail tip, colour and pattern. Analysis of mitochondrial cytochrome-b sequence data shows that *S. wyberba* sp. nov. represents an evolutionary lineage independent of the *S. swaini* populations of southeastern Queensland. □ *Saltuarius* *Squamata*, *Gekkonidae*, *granite-based forests*, *Queensland*.

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In their recent revision of *Saltuarius*, Couper et al. (1993) recognised four species: *S. cornutus*, *S. salebrosus*, *S. occultus* and *S. swaini*. That *Saltuarius* specimens from southeastern Queensland's 'granite belt' differ morphologically (size, proportion) and in colour and pattern from those from rainforests of southeastern Queensland is well documented (Covacevich, 1975; Couper et al., 1993). Couper et al. (1993) assigned them to one of three 'forms' of *S. swaini*. The 'heavily-blotched' form was recognised from 'dry eucalypt/granite habitats centred on the Stanthorpe area, SEQ, and the New England Tableland, NSW'. The rainforest populations of *Saltuarius* in southeastern Queensland belong to *S. swaini*. Those from the open forests of the Stanthorpe area, SEQ are not simply a 'form' of *S. swaini*. Previously-recognised morphological differences, supported by biochemical data, indicate that they belong to a distinct new species. The status of *Saltuarius* specimens from the New England Tableland, NSW remains enigmatic because of scant biochemical data from these populations. *Saltuarius* specimens from the granite habitats of SEQ are easily-separated from *S. swaini*. Recognition of this new species necessitates modification to the description of *S. swaini*, and to the previously published list of specimens referred to that species by Couper et al. (1993).

Morphological characters follow Covacevich (1975) and Couper et al. (1993). Skeletal definitions follow Bauer, (1990). The following abbreviations apply: snout to vent length (SVL); tail length (T), from posterior margin of cloaca to tip of tail; attenuated tip of original tail (TT); head

length (HL); head width (HW); head depth (HD) lower jaw to top of head, between eyes; snout length (S). Additional measurements include - length of front leg (L1) axilla to tip of longest digit; length of hind leg (L2) groin to tip of longest digit; neck length (NL) axilla to posterior margin of ear. Specimen designators: Australian Museum (AMR), Queensland Museum (QMJ) and South Australian Museum (SAM). Comparative material is listed in Appendices 1 and 2.

## SYSTEMATICS

### *Saltuarius wyberba* sp. nov. (Figs 1-3)

MATERIAL EXAMINED. HOLOTYPE: QMJ61541 (Fig. 1), Girraween NP, Granite Arch Trail, 1.5km from Bald Rock campground, granite boulders in open forest (28°50'S, 151°56.04'E) SEQ; C. Schneider, P. Couper, M. Lara & J. Girling; 11 Nov 1995. Tissues from this specimen have been lodged with the SAM. PARATYPES: AMR92121, R92123, 6km W of Amiens (28°34'S, 151°46'E) SEQ; AMR98332, Approx 1.5km NW of Amiens (28°34'S, 151°46'E) SEQ; QMJ35401, Boonoo Falls, via Tenterfield (28°48'S, 152°10'E) NSW; QMJ25374, Girraween NP, via Stanthorpe (28°50'S, 151°55'E) SEQ; QMJ28648-49, Girraween area, nr Wyberba (28°50'S, 151°55'E) SEQ; QMJ29115-J29117, Stanthorpe area, ?Girraween (28°50'S, 151°55'E) SEQ; QMJ30677, Stanthorpe, Aztec Temples, nr Underground R (28°50'S, 152°05'E) SEQ; QMJ-27349, Girraween NP, nr (28°50'S, 151°55'E) SEQ; QMJ51633-J51636, Girraween NP, Natural Arch track (28°50'S, 151°55'E) SEQ; QMJ51093, Girraween NP, edge, outside park (28°50'S, 151°56'E)

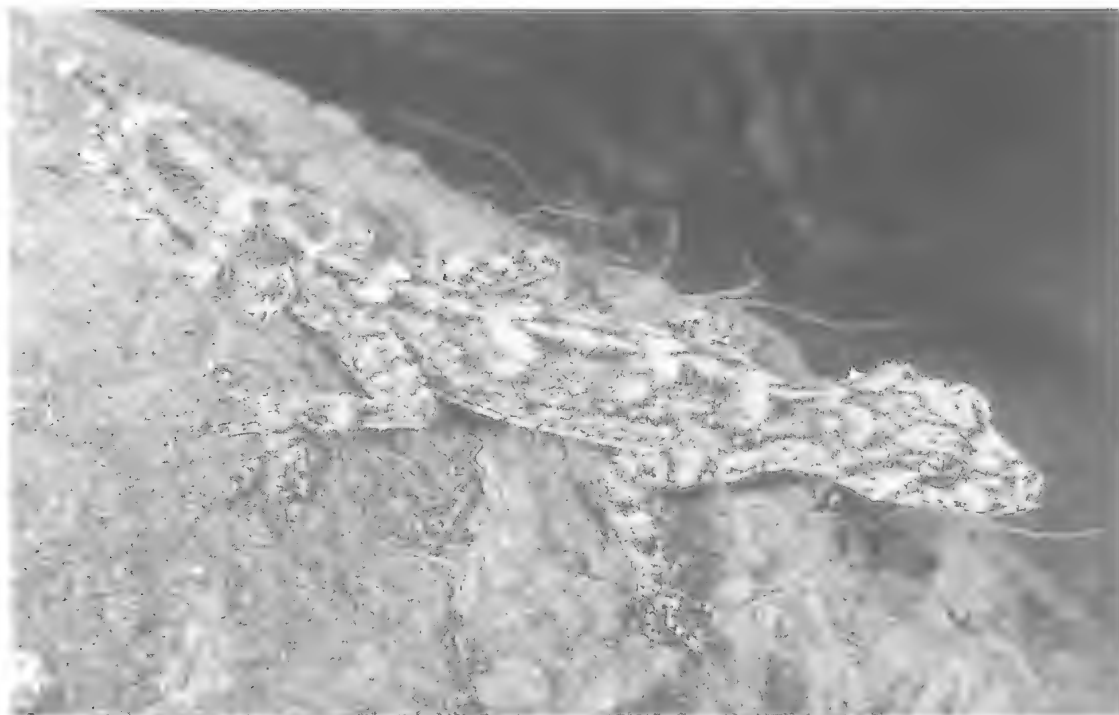


FIG. 1. The holotype of *Saltuarius wyberba* sp. nov. (QMJ61541).

SEQ; QMJ61539-40, J61542-45, Girraween NP, Granite Arch Trail, 1-5km from Bald Rock campground (28°50', 151°56.04') SEQ; QMJ50345, Girraween NP (28°51'S, 151°55'E) SEQ; QMJ54847, Bookookooara, Boonoo SF (28°51'S, 152°11'S) NSW; QMJ30420, Wyberba, nr (28°52'S, 151°52'E) SEQ.

**ETYMOLOGY.** Wyberba is a rail-siding on the western boundary of Girraween National Park, in the Stanthorpe area, SEQ. The name is reported to be of Aboriginal origin, and said to mean 'at the end of the mountain' (Harslett & Royle, 1980). The epithet is to be treated as a noun in apposition.

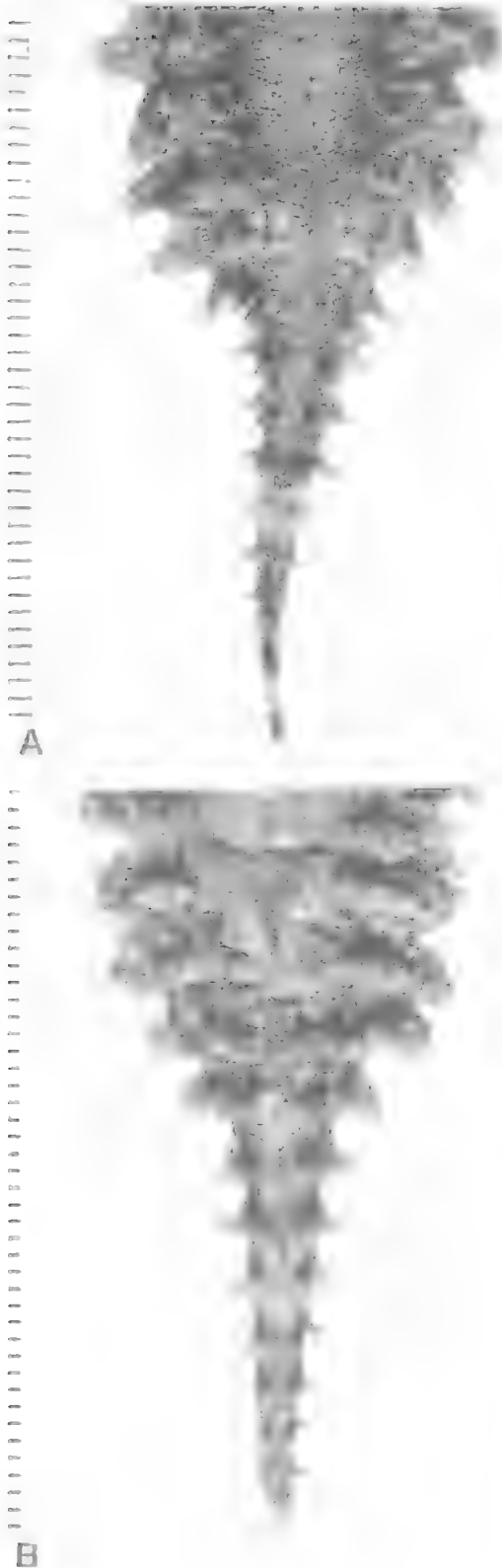
**DIAGNOSIS.** *Saltuarius wyberba* sp. nov. is distinguished from *Saltuarius* spp. except *S. swaini*, in lacking male preanal pores. *S. wyberba* is separated from *S. swaini* by size (max SVL 109.2mm vs 131mm); in being more dorsoventrally compressed (mean HD 38% HW  $n=26$  vs 45%  $n=35$ ), and by the shape and spinosity of the attenuated tail tip (finely tipped with only minute tubercles, Fig. 2a vs bluntly tipped with large tubercles, Fig. 2b). Colour pattern also distinguishes these two species. *S. wyberba* is grey to tan, with a pale vertebral stripe and heavy brown to black blotching. *S. swaini* is grey or mid-dark brown with lichen-like, dark-edged,

dorsal blotches or grey/brown with a pale vertebral streak. *S. wyberba* has a wide, open V-shaped marking between the eyes (Fig. 3a). In *S. swaini* this is a narrow deep V (Fig. 3b).

**DESCRIPTION.** SVL(mm): 75.4-109.2 ( $n = 27$ , mean = 95.2). Proportions as % SVL: T = 68.4-80.9 ( $n = 11$ , mean = 72.4); TT = 26.8-32.4 ( $n = 11$ , mean = 29.4); L1 = 40.1-51.6 ( $n = 25$ , mean = 44.9); L2 = 51.0-59.7 ( $n = 24$ , mean = 55.3); HL = 26.4-29.5 ( $n = 27$ , mean = 27.8); HW = 20.5-23.7 ( $n = 27$ , mean = 22.3); HD = 7.2-9.7 ( $n = 26$ , mean = 8.5); S = 11.0-12.9 ( $n = 27$ , mean = 12.1); NL = 15.6-21.9 ( $n = 25$ , mean = 19.4).

**Head.** Large, depressed, triangular, distinct from neck; covered in small granules which are intermixed with large rounded to conical tubercles; skin of head coossified with skull; rostral completely divided by a single deep groove ( $n = 26$ ), or almost completely divided ( $n = 1$ ); rostral contacting nostril; ear opening elliptical, vertical, much less than half as large as eye; supralabials 13-18 ( $n = 54$ , mean = 14.6); infralabials 10-14 ( $n = 54$ , mean = 12.2); Tongue colour in life, grey/purple.

**Neck.** Moderate to broad, 31-48% HW.



Body. Moderate, depressed, covered in small granules; dorsal granules intermixed with larger conical tubercles; tubercles moderate to large on back, flanks and neck; lower flank tubercles small to large, sometimes associated with a lateral flange running from axilla to groin; basal scales surrounding flank tubercles slightly enlarged; granules on throat noticeably smaller than those on chest and belly.

Preanal pores. Absent.

Limbs. Long, covered in pointed tubercles dorsally; digits strong, compressed distally; subdigital lamellae (fourth toe) 18-24 ( $n = 54$ , mean = 20.4).

Original tail. ( $n = 11$ ) Depressed, broad and contracted at base and attenuated at tip; anterior flared portion surrounded by an undulating flange which bears slender, sharply pointed tubercles around its margin; dorsal surface of tail (except along midline of flared portion) covered in large conical tubercles which are particularly pronounced on the attenuated tip; tail tip slender and free of tubercles, or with only minute tubercles; number of rows of enlarged spinose tubercles anteriorly across the attenuated tip 4-6 ( $n = 11$ , mean = 5.5); attenuated tip accounts for 38-45% of total tail length; ventral surface smooth with a shallow groove along the midline of attenuated tip.

Regenerated tail. ( $n = 11$ ) Depressed, broad and leaf-like contracted at base and only just attenuated at tip; tail margin is a broad, thin flange which bears minute spinose tubercles around the edges; tail free from spinose tubercles on both dorsal and ventral surfaces; ventral surface without any indication of a shallow groove along the midline.

*Skeletal Features.* Supraocular portion of frontal grooved; anterior process of interclavicle not present; epipubic cartilage expanded; presacral vertebrae 25; sacral vertebrae 2; lumbar vertebrae 2; 1st autotomy septum 6; abdominal vertebrae bearing reduced ribs 4; rib free cervicals 3; cervical vertebrae not elongate; sternal ribs 3; mesosternal ribs 2; based on QMJ29115 (alizarin stained).

*Pattern (in spirit).* Dorsum tan or grey; heavily marked with dark brown/black or grey blotches on head, body and limbs; a narrow vertebral

FIG. 2. Attenuated, original tail tips of the *Saltuarius* species. A, *S. wyberba* (QMJ61541), with a finely tipped tail, and only minute tubercles; B, *S. swaini* (QMJ5649), with a bluntly tipped tail, and large tubercles.

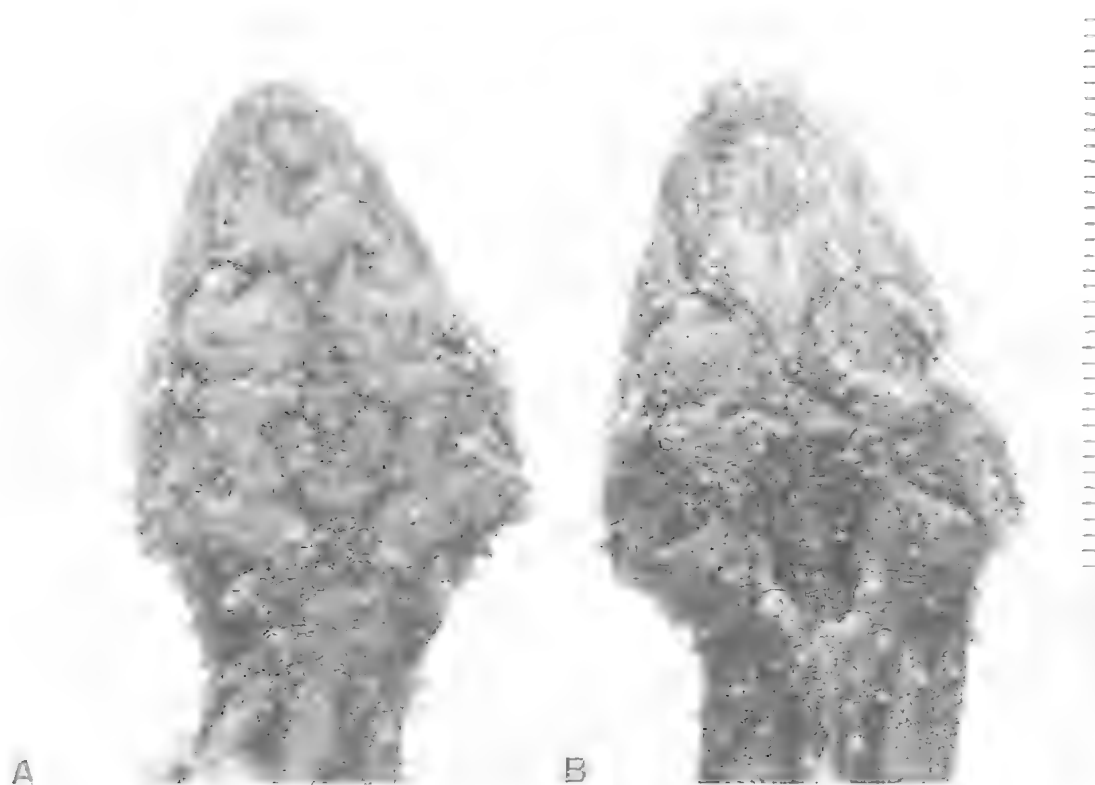


FIG. 3. Markings between the eyes in the *Saltuarius* species. A, *S. wyberba* (QMJ61541), with a wide, open 'V'; B, *S. swaini* (QMJ51638), with a narrow, deep 'V'.

stripe, broken by four irregular tan or grey blotches, extends from neck to base of tail; a wide, open V-shaped marking between the eyes (Fig. 3a); labials light grey, mottled with dark brown; toes prominently marked by alternating pale and dark crossbands. Venter cream with clusters of dark brown granules which often form irregular bars below the infralabials, and on the anterior margin of the thigh. Original tail grey to tan above, marked with four to six irregular pale crossbands which extend to the ventral surface on the attenuated tail tip; cream to pale grey below, mottled with brown, and with a series of pale blotches along the midline of the anterior flared portion. Regenerated tail pale grey, or tan with darker marbling.

*Measurements and Scale Counts.* Holotype (QMJ61541): SVL(mm): 97.56, T = 69.55, TT = 26.19, L1 = 43.0, L2 = 53.6, HL = 26.0, HW = 21.0, HD = 8.2, S = 11.6, NL = 17.2, supralabials 13/13, infralabials 13/12, subdigital lamellae (4th toe) 22/22.

## GENETICS

Analysis of mitochondrial cytochrome-b sequence data supports the recognition of *Saltuarius* populations from granite habitats in the Stanthorpe area (28°40'S, 151°56'E) SEQ, as distinct from *S. swaini* sensu stricto. 372 base pairs of the 5' end of the light strand (and corresponding heavy strand) of the cytochrome-b gene were sequenced from 7 individuals from Girraween National Park (28°50'S, 151°55'E), near Stanthorpe, and compared with homologous sequences from all species of leaf-tailed geckos including 2 individuals representing *S. swaini* from Lamington National Park (28°14'S, 153°08'E) and Mt Tamborine (27°58'S, 153°11'E). Amplification of target DNA was achieved from CsCl gradient purified mtDNA and/or total genomic DNA extracts with primers Ph-1 and MVZ04 (primer sequences available from CJS). PCR was performed in 25 l reactions with 1.5mM MgCl<sub>2</sub>, 0.5U Taq polymerase (Promega), 1X Promega Thermobuffer, 60M each dNTP, 0.2M each primer, and 30 cycles with 45

seconds at 94°C, 45 seconds at 45°C, and 45 seconds at 72°C. Automated sequencing of double-stranded products followed manufacturer's (ABI) suggested protocols. Analyses are those of one of us (CJS), unpub. data. Phylogenetic analysis reveals that Girraween sequences form a strongly supported sister group to a monophyletic group — composed of the Lamington-Mt Tamborine sequences (100% of bootstrap replicates in parsimony analysis with all characters unordered and equally weighted). Sequences from the Girraween group differ from the Lamington-Mt Tamborine group at 13.8% of sites, a level of difference similar to that among species of the closely related genus *Phyllurus* (*P. isis*, *P. nepthys*, and *P. ossa* differ at 10.0–13.9% of homologous sites). These data, in combination with morphological differences indicate that the Girraween NP *Saltuarius* populations represent an evolutionary lineage independent of the Lamington-Mt Tamborine populations.

Tissue samples from *Saltuarius* specimens from localities in New South Wales are scant. However, tissues (AMR141964–5, tissue sample numbers NR878–9) were obtained from specimens in two populations of *Saltuarius* at Chelundi State Forest (30°01'07"S, 152°30'02"E & 30°03'04"S, 152°21'36"E), NSW. Chelundi SF is near Guy Fawkes NP, approximately 145 kms SW of Girraween NP. Cytochrome-b sequences from these individuals differ slightly from each other (0.5%) and form a sister group to the *Saltuarius* populations of Girraween NP, SEQ. Importantly, these sequences differ from the Girraween samples at approximately 11% of sites and from Lamington-Mt Tamborine, SEQ sequences at 12.6–13.1% of sites. Given the level of sequence differences and the discontinuity of suitable habitat, it seems unlikely that the Chelundi and Girraween populations are conspecific. However, in the absence of comprehensive data, their status remains uncertain.

## REMARKS

Populations of *S. wyberba* from the granite-based forests of the Stanthorpe area, SEQ are morphologically and genetically distinct from populations of *S. swaini* occurring in the rainforests of southeastern Queensland. Specimens QMJ53984, AMR141964–65, AMR43870, AMR123490 and AMR149768, listed in Appendix 2, are of uncertain status. Morphology and colour-pattern of these specimens readily separate them from *S. swaini*. Although they are sim-

ilar in some respects to *S. wyberba* (colour/pattern) they have been excluded from the type series because morphological variations set them apart from *S. wyberba* from SE Queensland. (Specimen QMJ53984, Mann R. Nature Reserve, NSW, has large, scattered granules intermixed among the small granules of the chin. There is no evidence of this character in any of the specimens from the Stanthorpe area). *Saltuarius* specimens similar in colour and pattern to *S. wyberba* have been recorded from dry, open forests associated with granite as far south as Armidale, 30°31'S, 151°40'E (H. Hines pers. comm.). The possibility that isolates of granite-based forest in N NSW may support several species of *Saltuarius* is not without precedent. In a recent review, Couper et al. (1993) described three new species of *Phyllurus* from rainforests in coastal, mid-eastern Queensland. All occur in extremely close proximity on rainforest-covered mountains, their populations being separated by narrow corridors (9–30 km) of open forest. Two of these species (*P. nepthys* and *P. ossa*) may be sympatric in the Clarke Ra. A parallel situation may occur in the granite-based, open forest habitats of SE Queensland and N NSW (28°40'–30°31'S). Here, exposed granite occurs as isolated outcrops and distinct gorge systems in a 'sea' of dry, open forest (New England hardwoods). It seems possible that each separate 'island' may also support a distinct *Saltuarius* sp. Assessment of the status of these *Saltuarius* populations hinges on extensive collecting and genetic sampling throughout the 'granite belt' of SE Queensland and N NSW.

Although *S. swaini* sensu stricto appears to be a rainforest species, it may occur in sympatry with *S. wyberba* in granite-based open forests in the Amiens region (28°34'S, 151°46'E), SEQ. A single specimen (AMR92122) morphologically indistinguishable from *S. swaini*, has been collected from '6 km NW Amiens' (Couper et al., 1994). Available data suggest *S. swaini* is an obligatory rainforest species, with the exception of this enigmatic specimen. There is no reason to question data associated with AMR92122. Ross Sadlier of the Australian Museum (in litt., 23 April, 1996) regards the collector of this specimen as supplying data that was 'usually better than average'. Specimen AMR92122 has been formalin-fixed. Attempts to extract useable DNA for a genetic assessment of this specimen were unsuccessful.

*S. SWAINI* SENSU STRICTO

With the recognition of *S. wyberba*, the following changes apply to the description of *S. swaini* Wells & Wellington (Couper et al, 1993). Material examined: specimens QMJ35401, QMJ24250, QMJ27349, QMJ25374, QMJ28648-9, QMJ29115-7, QMJ30677, QMJ51093, QMJ51633-6, QMJ54847, QMJ50345, QMJ30420, AMR92121, AMR92123, AMR98332, AMR110510 are *S. wyberba*, not *S. swaini*. Specimens QMJ53984, AMR141964-65, AMR43870, AMR123490 and AMR149768 (Appendix 1) are *Salvatorius* sp. incerta cedis. Morphology: *S. swaini* has a deep head (mean head depth 45% HW) and the attenuated tail tip has large spines, and terminates bluntly (Fig. 2b). Meristics: the range for each measurement provided by Couper et al. (1993) remains unchanged (all measurements for *S. wyberba*, except HD, fall within the range previously given for *S. swaini*). Colour/pattern: two principle colour forms exist: 1) grey-medium brown with both paler and darker blotches in the base colour; these blotches are edged with brown or black lines to give a 'lichen-like' effect; often with a pale vertebral streak. 2) grey or mid-dark brown with a pale vertebral streak.

## ACKNOWLEDGEMENTS

The authors thank the Co-operative Research Centre for Tropical Rainforest Ecology and Man-

agement and the Centre for Conservation Biology, University of Queensland; the Queensland Museum; Ross Sadlier (Australian Museum), Harry Hines, Guy Hodgson (NSW National Parks and Wildlife Service), Noel Cortinas, Kate Couper, Amy Couper, Jenny Faulkner, Janie Girling, Marcia Lara, Mary Mulcahy, Simon and Jenny Ormsby Jeff Wright, Steve Wilson and Lauren Keim, who assisted us in the preparation of this work.

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## APPENDIX 1.

Specimens of *Salvatorius swaini* examined in the current study. All localities are for Queensland unless otherwise indicated.

QMJ398, J2409, J2933-34, J3254, J4439, J8183, J8359, J8861, J10440, J12257, J51095 Mt Tamborine, (27°55'S, 153°10'E); J4819, Mt Tamborine, Eagle Heights (27°55'S, 153°12'E); J148 Canungra Ck (27°58'S, 153°09'E); J3215 Canungra (28°01'S, 153°11'E); J4198, J5690 Mudgeeraba (28°05'S, 153°22'E); J5649 Flying Fox Valley, Beechmont (28°08'S, 153°12'E); J3313 Tallebudgera (28°08'S, 153°26'E); J5382 Lamington NP (28°12'S, 153°05'E); J8646 Lamington NP Binna Burra (28°12'S, 153°11'E); J51094 Mt Superbus SF, via Warwick, (28°13'S, 152°28'E); J51637-40 O'Reilly's, Lamington NP (28°14'S, 153°08'E); J23937 near Mt Ballow, (28°16'S, 152°37'E); J8074, J8075 (allazarn stained), J8099 Mt Clunice, via Boonah (28°18'S,

152°32'E); J1143 Tweed R. (28°18'S, 153°27'E) NSW; J5757 Chillingham, Murwillumbah (28°19'S, 153°17'E) NSW; J10565 Mt Lindesay (28°23'S, 152°43'E) SEQ; J54846 Bray's Ck, Border Ranges NP (28°24'S, 153°03'E) NSW; J9054 Bulahdelah, 96km NE Newcastle (32°25'S, 152°12'E) NSW.

## APPENDIX 2.

Specimens of uncertain status from granite habitats in NSW, QMJ53984, Teapot Ck, Narrow Pass Fire Trail, Mann River Nature Reserve (29°45'S, 152°02'E) NSW; AMR141964, Chaelundi SF, (30°01'07"S, 152°30'02"E) NSW; AMR141965, Chaelundi SF, Sundew Lookout (30°03'04"S, 152°21'36"E) NSW; AMR43870, 35km E. of Guyra (30°15'S, 152°00'E) NSW; AMR123490, Tullawudjah CK, NSW; AMR149768, Black Ck, 6.1km SE along Black Hole Trail, Curramore SF (29°30'30"S, 152°11'24"E) NSW.



## NEW SPECIES OF RHIZOPINE CRABS (CRUSTACEA: BRACHYURA) FROM NORTHERN AUSTRALIA

PETER J.F. DAVIE AND ANDREW HUMPHERYS

Davie, P.J.F. & Humpherys A. 1997 06 30: New species of rhizopine crabs (Crustacea: Decapoda: Pilumnidae) from northern Australia. *Memoirs of the Queensland Museum* 42(1): 97-103. Brisbane. ISSN 0079-8835.

Two new species of rhizopine crabs are described from Australia. *Cryptolutea arafurensis* sp. nov. is described from Darwin and the Gulf of Carpentaria. It is distinguished by the degree of carapace granulation and the prominent anterolateral teeth. *Heteropilumnus longisetum* sp. nov. is only known from the North-West Shelf. It is related to other *Heteropilumnus* species with a coat of long fine setae on their carapace, legs and claws. □ *Brachyura, Pilumnidae, Rhizopinae, Cryptolutea, Heteropilumnus, Australia.*

P.J.F. Davie & A. Humpherys, Queensland Museum, P.O. Box 300, South Brisbane, Queensland 4101, Australia; 3 April 1997.

Scientific cruises conducted by the Commonwealth Scientific and Industrial Research Organisation (CSIRO) in northern Australian waters in recent years have produced a large number of brachyuran specimens. Among the material deposited in the Queensland Museum from these cruises are several species of pilumnid crabs of the subfamily Rhizopinae. Two of these species are considered new to science and are treated in this paper.

In the most recent revision of rhizopine taxonomy, Ng (1987) has redefined the concept of the Rhizopinae and removed it from the Goneplacidae and placed it in the Pilumnidae. A number of genera formerly considered rhizopine have been excluded, and *Heteropilumnus*, *Pseudolithochira*, *Luteocarcinus*, *Rhizopoides* and *Zehntneria* have been added to the group (see also Ng (1990) and Ng & Davie (1991)). It is in the context of this revised concept of the Rhizopinae that the new specimens from northern Australia are treated.

The Rhizopinae have been poorly documented in Australian waters and many specimens have remained unidentified or unrecorded. While this preliminary paper documents two new species, a later paper will attempt to fully document the Australian rhizopine fauna.

Specimens have been deposited in the Queensland Museum (QM) or the Northern Territory Museum (NTM). All measurements are in millimetres (mm) and are of maximum carapace width followed by length, unless otherwise stated.

### SYSTEMATICS

Family PILUMNIDAE Ortmann, 1893

Subfamily RHIZOPINAE Miers, 1886

*Cryptolutea arafurensis* sp. nov.

(Figs 1, 2)

MATERIAL EXAMINED. HOLOTYPE: NTM Cr001279, ♂ (16.7 x 13.4mm), Ludmilla Ck., Darwin, in mangroves, at low water, J. Hanley, 26.2.1982. PARATYPES: NTM Cr001279, ♂ (13.7 x 10.8mm), CSIRO Torres Strait, 7.3.1989. QMW21401, 3 ♂♂ (18.0 x 14.3, 19.5 x 15.6, 17.2 x 14.1mm), 2 ♀♀ (16.0 x 12.6, 16.9 x 13.3mm), 13°02'S, 139°22.2'E, Gulf of Carpentaria, 58m, dredged, CSIRO F.R.V. Southern Surveyor, 24.11.1991. QMW21402, ♂ (13.0 x 10.7mm), 2 ♀♀ (16.6 x 13.2, 13.1 x 10.7mm), data as for QMW21401. QMW21403, 7 ♂♂ (16.5 x 13.2, 16.6 x 13.5, 15.1 x 12.0, 17.2 x 13.7, 13.7 x 11.2, 15.5 x 12.3, 14.7 x 11.5mm), 12°10.5'S, 139°56.7'E, Gulf of Carpentaria, 59m, dredged, CSIRO F.R.V. Southern Surveyor, 24.11.1991. QMW21400, ♂ (14.2 x 11.7mm), 2 ♀♀ (15.5 x 12.4, 16.8 x 13.6mm), 13°25.6'S, 138°36'E, dredged 54m, CSIRO F.R.V. Southern Surveyor, 24.11.1991.

DESCRIPTION. Carapace subquadrate, c. 1.22 times broader than long, somewhat vaulted anteriorly. Dense covering of tomentum present on entire dorsal surface. Carapace surface minutely punctate in central regions; minutely granular towards lateral and posterior margins or nearly smooth in some specimens. Dense scattered tufts of tomentum, of varying density, particularly in anterior third and towards the lateral margins. Carapace regions relatively poorly defined; overlying fine pubescence obscuring surface detail in some specimens. Metagastric grooves well indicated together with forked frontal groove. Sub-

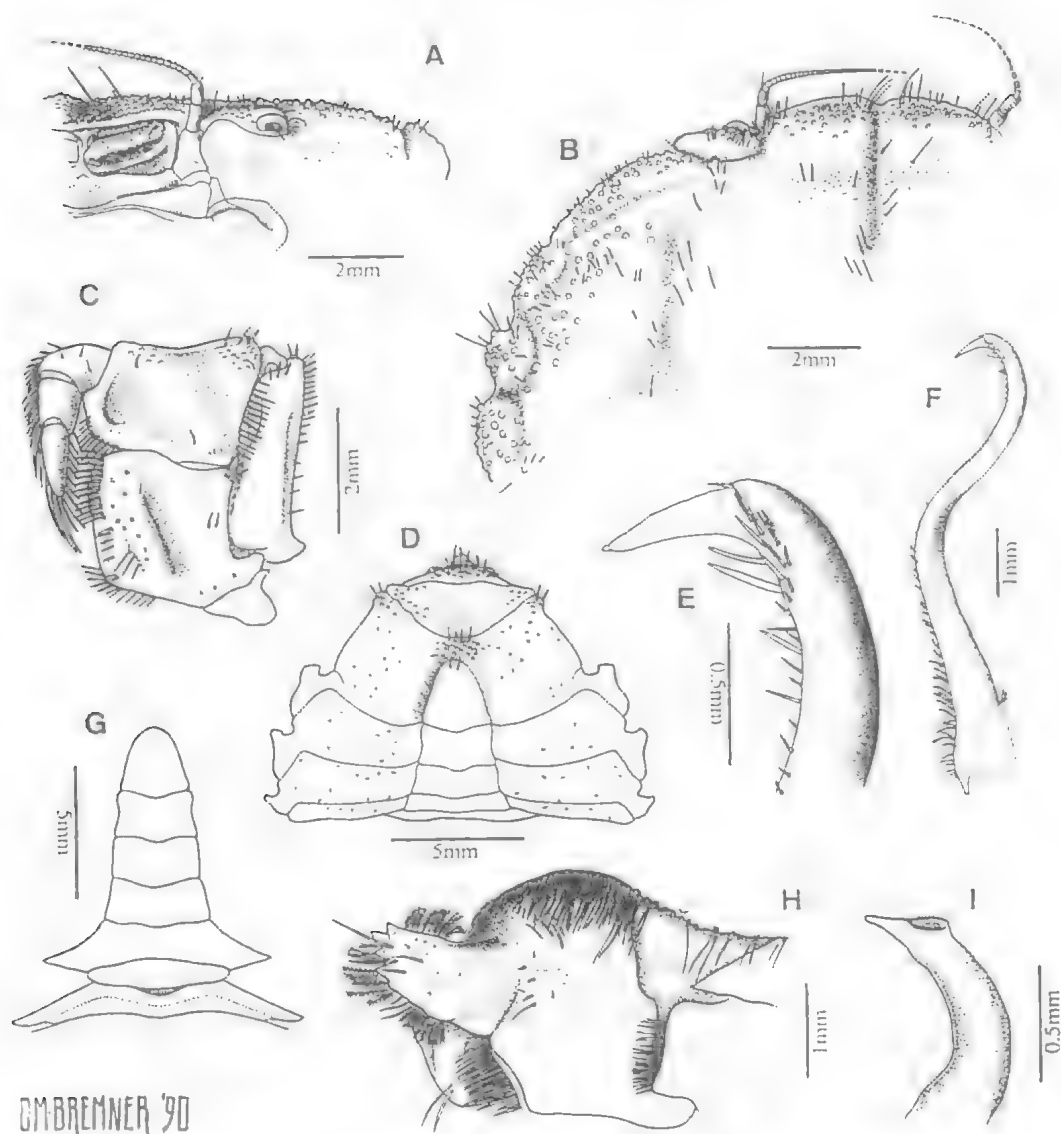


FIG. 1. *Cryptolutea arafurensis* sp. nov., holotype, NTM Cr001279, ♂ (16.7 x 13.4mm). A, frontal view; B, frontal and anterolateral margins; C, 3rd maxilliped; D, sternum; E, F, 1st gonopod; G, abdomen; H, coxal plate of pereopod 5; I, 2nd gonopod.

hepatic lobes well marked. Front deflexed, frontal margin bilobed, a median cleft with groove present; margins fringed with fine setae. Orbits small and shallow but visible from above. Infraorbital margin entire, with internal angle somewhat acute. Ocular peduncles short, bulbous, immovable; cornea darkly pigmented and terminal. Antennules relatively short, folding into oblique fossae. Antennae with basal joint short, flagellum in contact with orbits. Epistome of

moderate length, shallow. Anterolateral margins convex, lobes partially obscured by fringing tomentum; exorbital angle rounded, first anterolateral lobe obtuse, scarcely indicated by shallow notch; following two lobes much more acute and separated by fairly wide U-shaped notches. Posterolateral margins sub-parallel. Subhepatic and pterygostomial regions smooth, but with a few clumps of setae.

Chelipeds subequal, somewhat robust; right cheliped usually larger than left; merus compact and high, trigonal; upper and lower margins fringed with fine setae; outer surface minutely granular; acute tooth present on upper margin. Carpus subovate, outer and upper surface granulate with scattered, long setae; inner surface smooth; prominent obtuse tooth present on interior margin; outer surface covered in fine setae. Palm broad, high and flat, upper and lower margins somewhat keeled; outer surface with conspicuous rows of tuberculate granules, more closely aggregated towards upper margin and sometimes sparse or nearly absent in some specimens; woolly tomentum overlying portions of upper and lower margins and adjoining areas. Index straight or slightly deflexed, with median carina; distal 1/3 usually smooth; lower margin fringed with fine setae. Gape with strong dentition. Dactylus downcurved, with a comb of setae on upper proximal margin, distal end without setae. Hooked tips of chelipeds overlap when closed. Distal 2/3 of index finger and dactylus dark sepia in colour (after preservation).

Ambulatory legs of moderate length, relatively stout and fringed with fine setae. Dactyli styli-form, heavily setose. Large projecting serrate plate present on upper surface of coxae of all 4 pairs.

Buccal cavern sub-quadrate. Third maxillipeds incompletely close buccal cavern. Ischium quad-rangular, outer surface smooth. Merus sub-quad-rate, smaller than ischium; anteroexternal angle strongly produced.

Thoracic sternum punctate. ♂ abdomen evenly tapered and heavily tomentose; with 7 distinct segments; segment 1 covering entire interspace between last pair of ambulatories; segment 2 much shorter; segment 3 longer again, with some-what acute lateral angles; segments 4-6 with con-cave margins; telson triangular with rounded apex.

Male genital pore coxal, exposed penis lying in channel between 4th and 5th thoracic sternites. Male gonopod sigmoid-shaped, with hooked tapering terminal portion.

**DISTRIBUTION.** Darwin, N.T. and the Gulf of Carpentaria; from low-water to 59m depth.

**ETYMOLOGY.** Name refers to the Arafura Sea.

**REMARKS.** This relatively large species is the 5th in the genus *Cryptolutea* to be described. This genus is characterised by the presence of a serrate plate on the coxae of the ambulatory legs.

*Cryptolutea arafurensis* sp. nov. is relatively common in the samples from the Gulf of Carpentaria, being the dominant species of Rhizopinae found. It is, however, highly variable in the degree of granulation on the carapace and cheliped palm, and in the extent of setation. Several specimens exhibited a markedly pubescent carapace whilst others were almost devoid of setae. Similarly, granulation in varying degree was present on the carapace of most specimens, but completely absent on some.

*Cryptolutea arafurensis* sp. nov. is distinguish-able from its congeners by the prominent antero-lateral teeth, and by the degree of carapace granulation typically present. In *C. lindemanen-sis* Ward, 1936, the carapace is relatively smooth and the anterolateral margins have less prominent teeth; the anterolateral lobes of *C. teschi* (Serène, 1971) are more tuberculate and less clearly sepa-rated as teeth than those of *C. arafurensis*. In addition the carapace of *C. teschi* appears more areolate or rugose than the present species. *C. granulosa* (MacGillchrist, 1905) is more evenly granulose, particularly on the outer surface of the palm, than the present species, and the dense tomentum on the dorsum is absent.

*C. sagamiensis* (Sakai, 1935) appears closest to *C. arafurensis* but it can be distinguished by the following characters: 1) the anterolateral teeth are more prominent, with the last 2 lobes narrower and showing a tendency to unite with each other; compared with the last 2 lobes being prominent, somewhat acute, and clearly separated from each other in *C. arafurensis*, 2) the larger number of granules on the outer surface of the cheliped palm, 3) in *C. sagamiensis* the merus and carpus of the chelipeds are covered in rudimentary gran-ules, whereas in *C. arafurensis* the carpus, in particular, is covered in prominent vesiculous granules, 4) according to the text-fig. 16(a) of Sakai (1935), the merus and ischium of the 3rd maxillipeds are more rounded in *C. sagamiensis* than in *C. arafurensis*.

***Heteropilumnus longisetum* sp. nov.**  
(Fig. 3)

**MATERIAL EXAMINED.** HOLOTYPE: QMW21423, ♂ (7.5 x 5.3mm), North West Shelf, W. Australia, 19°29.6'S, 118°53.2'E, trawled 37-38m, 25.10.1983, T. Ward (CSIRO). PARATYPE: QMW14449, ♂ (5.6 x 4.0mm), North West Shelf, 02B6BT, 81-82m.

**DESCRIPTION OF HOLOTYPE.** Carapace 1.4 times broader than long; more or less flat across



FIG. 2. *Cryptolutea arafurensis* sp. nov., holotype, NTM Cr001279, ♂ (16.7 x 13.4mm). A, frontal view of chelipeds; B, dorsal view. Scale lines in mm.

the mesogastric and branchial regions although becoming convex laterally; convex fore and aft over frontal third. Entire surface covered in fine silky setae; moderately long posteriorly, becoming much longer anteriorly; longest setae form transverse fringe across frontal region, and are about 1/3 or more length of carapace. Regions

relatively poorly defined, with only meta/mesogastric region being moderately distinct. Anterior to frontal fringe surface with only very tiny setae; front deflexed, bilobed; most prominent medially; sinuous with obtuse, subacute preorbital angle. Supraorbital margin sinuous, microscopically granular, without fissures.

Infraorbital margin also minutely granular; slightly raised below proximal margin of cornea; inner margin without enlarged tooth or lobe, inner angle rounded, meeting distal margin of basal antennal joint. Antenna with basal segment just touching front; flagellum about as long as frontal setae; each segment armed with 2 or 3 short setae distally; terminal segment with few very long setae distally which make antennae appear much longer. Anterolateral margin consisting of 4 teeth, including exorbital angle. Exorbital angle small, sub-acute, with few small accessory granules on outer margin; 2nd tooth of similar size, leading margin very short, trailing margin long and with few microscopic granules; 3rd tooth most prominent, acute; 4th tooth smallest, clearly defined but little bigger than large acute granule. Greatest carapace width between 3rd anterolateral teeth. Posterolateral margin longer than anterolateral, straight, converging posteriorly. Posterior margin straight, with slightly raised rim.

Third maxilliped with merus c. 1.25 times wider than long and  $2/3$  as long as ischium; distal margin concave; ischium about as long as wide, inner margin produced, broadly convex and slightly crenulated.

Sternum and abdomen entirely covered with moderately long setae; ♂ abdomen reaching about half distance across fused 3rd and 4th thoracic sternites. ♂ abdomen as figured; telson with convex margins reaching a blunt point, longer than other segments and c. 1.7 times length of penultimate segment; segments 1 and 3 widest, similar in width, occupying entire space between coxae of last pair of legs; 2nd segment c. 0.7 times width of 3rd. ♂ 1st pleopod sigmoid; apical beak relatively long and acutely pointed, projecting laterally rather than recurved; armed with series of fine bristles on inside edge of distal curve.

Chelipeds subequal, right slightly more swollen; merus short, trihedral, unarmed except for row of sharp granules on upper inner border, and few smaller granules on ventral anterior margin. Carpus unarmed, inner angle bluntly pointed, covered in fine setae which are short proximally but very long distally; surface smooth beneath setae, without obvious sculpturing. Palm excluding fixed finger c. 1.25 times longer than high; fingers relatively long, fixed finger c. 1.1 times height of palm, markedly downturned, particularly on left cheliped; both fingers with tips pointed, margins with about 5 large, triangular, sharply crested teeth; dark colouring on teeth entire distally then extending obliquely backwards towards base of gape. Entire outer face of

palm covered in very long, fine, soft setae; surface scattered with granules difficult to see except along outer margins of fingers where they become more conspicuous, especially on left chela. Walking legs missing.

**Variation.** The smaller paratype male shows some significant variations from the much larger holotype, and is in possession of several walking legs. The carapace anterolateral angles are cut into much more prominent, triangular teeth, and the outer margin of the 2nd tooth appears comparatively shorter. The dark colouring on the fingers of the chelae is restricted to the distal ends, and does not extend backwards along the gape. The tip of the 1st pleopod is not as long and acute. Walking legs moderately long and slender; length of longest c. 1.6 times width of carapace, width of merus c. 0.3 times length; dactylus longer than propodus, tip curved and acute. Propodi, carpi and dactyli bear very long silken setae, particularly on outer borders. All segments unarmed except for a few sharp, irregular granules on the upper margin of the meri.

**DISTRIBUTION.** Only known from the North-West Shelf, Western Australia; in 37-82m depth.

**ETYMOLOGY.** Named in reference to the long setae covering the carapace, legs, and claws. It is used as a noun in apposition.

**REMARKS.** *Heteropilumnus* is a relatively large (18 recognised valid species) and taxonomically confused genus that is in need of a full revision. Despite this there are only a restricted number of species within *Heteropilumnus* that resemble *H. longisetum* sp. nov. in bearing a coat of long fine setae on their carapace, legs and claws. The closest in appearance to *H. longisetum* sp. nov. are *H. ciliatus* (Stimpson, 1858), *H. lanuginosus* (Klunzinger, 1913), *H. splendidus* (de Man, 1929) and *H. trichophoroides* (de Man, 1895). Comparing our new species with the figures of *Heteropilumnus ciliatus* given by Shen (1936: text-fig. 2 [as *H. cristadentatus* Shen, 1936]) and Sakai (1976: pl. 176, fig. 3) *Heteropilumnus longisetum* differs from *H. ciliatus* by the much lower, less prominent, anterolateral teeth; the more extensive covering of longer setae particularly over the posterior half of the carapace; and the outer distal margin of the merus of the 3rd maxilliped being not produced.

It differs from the original figures of *H. lanuginosus* (Klunzinger, 1913: pl. 2, fig. 18; pl. 7, fig. 4) by lacking the broad tooth on the inner margin of the infraorbital margin. *H. splendidus*

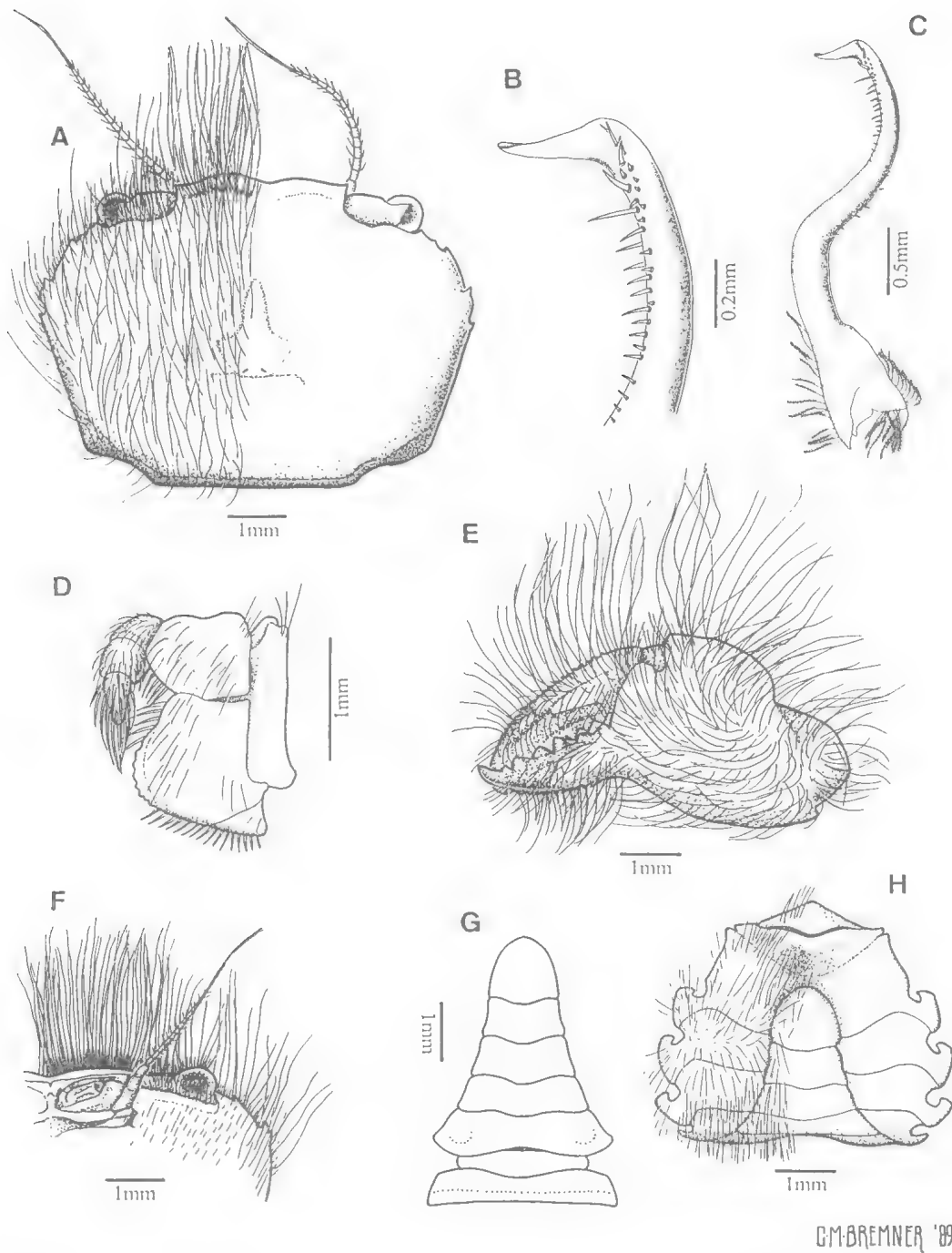


FIG. 3. *Heteropilumnus longisetum* sp. nov., holotype, QMW21423, ♂ (7.5 x 5.3mm). A, dorsal view of carapace; B, C, 1st gonopod; D, 3rd maxilliped; E, left chela; F, frontal view of orbit and antennae; G, abdomen; H, sternum.

can be easily separated because of its lack of clearly defined anterolateral teeth (see de Man (1929: pl. 1, fig 3-3c; pl. 2, fig. 3d-f). Finally it differs from *H. trichophoroides* (cf. figures of de Man (1895: 13, fig. 8a-e) and Rathbun (1910: fig. 40, pl. 1, fig. 8 [as *Pilumnus borradalei* Rathbun, 1909]) because the posterolateral margins are less convergent; the frontal margin is less produced; the regions on the carapace are much less defined; and the setae of the carapace are much longer.

#### ACKNOWLEDGEMENTS

We are grateful to Dr A.J. Bruce and Karen Coombes of the Northern Territory Museum, and to Trevor Ward of C.S.I.R.O., for the sending study specimens; Clare Bremner drew the excellent figures. The work could not have been done without the financial support of the Australian Biological Resources Study to P. Davie for the study of Australian xanthoid crabs.

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**COMBAT AND COPULATION IN *OXYURANUS MICROLEPIDOTUS* (ELAPIDAE).** *Memoirs of the Queensland Museum* 42(1): 104, 1997. Shine & Covacevich (1983) reviewed the ecology of *Oxyuranus* spp., largely from examination of museum specimens. However, while they were able to report body size and aspects of reproduction and feeding, combat between males and copulation were not described. Male vs male combat in Australian elapids is well known (Shine, 1991). It has been reported most recently (in *Demansia vestigiata*) by Covacevich et al., 1994. Such behaviour occurs in taxa characterised by male size superiority and is believed to be a strategy for forcing rival males away from a receptive female, defending against homosexual courtship and obtaining food ahead of a rival (Shine et al., 1981).

For *Oxyuranus* spp., accounts of combat/copulation are scant. Combat between ♂♂ *O. scutellatus* in the wild has been photographed (Shine, 1991) 'during the mating season'; and copulation has been observed in August and early December (Shine & Covacevich, 1983). Neither has been described previously in *O. microlepidotus*. In July–September, 1996 both combat and copulation were observed in wild specimens of *O. microlepidotus* in Astrebla National Park, 26km SE of No. 2 bore (at approximately 24°07'S 140°31'E, SWQ).

**Combat ♂♂.** Two specimens were encountered at approximately 17.22 hours, on 2 September, 1996 (Fig. 1; QM transparencies NR386, NR387, NR388). The snakes were fully entwined, 'plaited', as reported in black snakes by Shine (1978). Both specimens had their heads and approximately 40cm of their bodies raised from the ground and were frequently and alternately lashing out at each other. Their mouths were not and did not open. The snakes often came together with one head resting on the other. Their bodies were tightly coiled. What could be termed 'head-raising behaviour' frequently resulted in their falling suddenly to the ground, twisting and repeatedly rolling over one another. This behaviour continued for 30 minutes, when the snakes separated and moved slowly away. One went into a Bilby (*Macronis lagotis*) burrow nearby. The other followed the first to the burrow entrance, apparently searching. This second specimen then entered the same burrow. After 20 minutes one specimen surfaced from a different entrance, approximately 2m from the first. The other re-emerged from the initial burrow entrance and a similar ritual of entanglement and head-raising ensued for five minutes. Both specimens then entered the first burrow. About one minute later, the head of one specimen appeared from the second entrance. The specimen emerged from the burrow and moved across the plain rapidly. This occurred at 18:10 hours as the last 20–30cm of the other snake was 'disappearing' down the first entrance. At that time there was little light and observations ceased.

**Copulation ♂♀.** On 6 August, 1996, two specimens were observed 2m from a Bilby burrow at 13:30 hours. One (presumed ♂), was 'draped' in a series of coils over the sides of the other (presumed ♀), which was motionless. They were 'joined' genitally (Fig. 2; QM transparency NR389). The (presumed) ♂ frequently was contracting its body, giving the

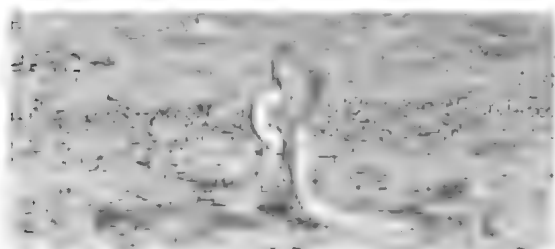


FIG. 1. Male *Oxyuranus microlepidotus* combat. (P. McRae)



FIG. 2. *O. microlepidotus* in copulation. (P. McRae)

impression that it was attempting to maintain its 'superior' position. Infrequently, every 5–10 minutes, the body of the (presumed) ♂ contracted in a series of 'quivers', also along the length of the body. After 10–15 seconds these culminated in a short, sharp series of (presumed) orgasmic contractions. This behaviour continued for about 1 hr. Then the specimens moved slowly to and down the Bilby burrow. Two to three seconds later, one specimen emerged from the burrow and moved quickly to the mating site. It then returned to the burrow. This occurred twice during the next 10 minutes. On the last occasion, the specimen remained in the burrow. Both specimens were below ground when observations ceased at 1500 hours.

These observations both concur with and vary slightly from previous reports of other elapid species. They conform with an observation (Shine, 1978) that elapids which are heavy and muscular hold their bodies upright during ♂♂ combat. That ♂♂ combat occurs in *O. microlepidotus* may be at variance with the observation that such behaviour is known only where ♂♂ are larger than ♀♀ (Shine, 1991). The difference between the body sizes of ♂♂ vs ♀♀ *O. microlepidotus* has not been shown to be statistically significant (Shine & Covacevich, 1983). However, the sample (♂♂ 13, ♀♀ 6) was small. Copulation by *O. microlepidotus* in the wild in August is consistent with the timing of this behaviour in captive specimens.

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 P.D. McRae, Queensland Department of Environment, PO Box 149, Charleville, Queensland 4470, Australia; J.A. Covacevich, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 7 April 1997.

## TEMPORAL SEGREGATION OF HUMPBACK WHALES DURING MIGRATION IN SOUTHERN HEMISPHERE WATERS \*

W.H. DAWBIN

Dawbin, W.H. 1997 06 30: Temporal segregation of humpback whales during migration in southern hemisphere waters. *Memoirs of the Queensland Museum* 42(1): 105-138. Brisbane. ISSN 0079-8835.

All available data on post-war catches and some pre-war catches of humpback whales in the southern hemisphere between 66°S and 1°S have been examined for evidence that some age or reproductive categories migrate north, and south early in the season, while others follow in sequence later. The categories that showed significantly different time sequences between groups in non-polar waters were as follows:- all immature humpbacks (no significant difference between males and females), mature males (regardless of size), and mature females subdivided according to reproductive stage as pregnant, lactating or resting. Based on the average intervals between the mean dates for each category at whaling localities between 41°S (Cook Strait, New Zealand) and 1°S (Congo), lactating females accompanied by weaning 'yearlings' migrate north earliest and are followed by immature humpbacks, mature males, together with resting females and finally pregnant females at 12, 20, 23 & 31 days later respectively. During the return migration southwards, mixed females (including those in early pregnancy) occur first together with immature whales, and are followed by mature males and females in early lactation 10 and 16 days later. Reasons for believing these time intervals to be minimal are discussed. In general, humpbacks appear to return south in the same order in which they travelled north, but some females change status so that those that travel north early when near the end of lactation, may return south early as pregnant animals. Others that travel north late as pregnant animals, return south late as cows accompanied by young calves. Mature females, when pregnant, appear to spend a prolonged period in Antarctic waters but when suckling a calf they spend a substantially reduced interval in cold waters. Antarctic catches appear to have been taken over too short a season to demonstrate sequences during the entry and exit of humpbacks to Antarctic waters. □ *Humpback, Megaptera, southern hemisphere, migration, segregation.*

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The published information on the main features of humpback whale migrations between warm water breeding regions and cold water feeding regions have been described and reviewed by a number of workers. These are referred to by Dawbin (1966), so the present account will be confined to a discussion of segregation during the migratory cycle of humpbacks.

Ever since the International Whaling Statistics began publishing tables which classified the sex and sizes of whales caught in all main whaling grounds, it has been clear that there is a marked disparity in the composition of humpback catches from Antarctic regions as compared with those from temperate and tropical regions. While females usually predominate in Antarctic catches, males tend to predominate in catches from warmer waters. This change of composition suggests that the humpback population does not remain homogeneous throughout the season, but undergoes some degree of segregation into sex

and possibly age groups at certain phases of its seasonal movements. Mackintosh (1942) has discussed evidence of changes in the composition of humpback catches (inter alia) during the Antarctic season, but accounts of sequential changes in composition in other southern hemisphere regions have tended to describe movements in rather localised areas.

Segregation between whale categories may occur in space (geographical segregation) or in time. Geographical segregation is here regarded as the entry of one sex, age or other specified class within a species, to an area which is not entered by other classes of that species. The classes are then clearly separated in space. In time segregation, one or more classes enter an area at an earlier date than the other classes, but the latter enter the same area at a later date. At any one moment the classes may be separated in space but they all pass through the same area although at different times.

\* This work was completed in 1963, the year in which the International Whaling Commission banned the taking of southern hemisphere humpback whales.

Sperm whales provide an excellent example of geographical segregation. Mature males only are found at high latitudes while females and immature animals do not occur south of about 45°S. There are differences in sex ratios and in the proportion of mature and immature humpbacks represented in catches at different latitudes, but there are no known cases of such marked geographical segregation between categories of humpbacks as occurs with sperm whales. However, at many localities there are regular differences in the catch composition with change in season.

It is suggested that many of these cases may be the result of some humpback categories migrating to warm waters early in the season while others travel at varying intervals later. Any such tendency would change the relative proportions of those remaining after the start of migration as well as cause sequential changes in the composition of the stock migrating past any fixed point.

The object of the present study is to identify the reproductive stage of each humpback and relate this to the arrival time of each animal at specified latitudes during the migratory cycle. It is an attempt to specify the reproductive or age categories that tend to migrate earliest in the season and to determine the time interval between that of their peak density and that of categories which migrate at a later date. As part of time segregation, the order in which specified categories travel and the mean interval between categories is referred to in this account as 'time sequence'. It is this as distinct from geographical segregation that is the main subject of the present study.

## MATERIAL AND METHODS

With the exception of sighting records on cows accompanied by calves, humpbacks cannot be classified accurately into size, sex, or reproductive stage categories by observations at sea. Catch data on animals processed at whaling stations or factory ships have been published regularly in International Whaling Statistics, but the data are grouped into monthly categories or into size categories unrelated to dates. The object of the present study has therefore necessitated an analysis of the available data on individual humpbacks for those cases that specify the length, sex, stage of pregnancy, geographical position and date of catch.

**MATERIAL EXAMINED.** Data have been obtained for each of 65,600 humpbacks caught in the southern hemisphere. Of these 38,100 were caught in post-war

years and 27,500 were caught in pre-war years. Both samples include catches from Antarctic through to equatorial waters.

From temperate and tropical waters the post-war data relate to 28,243 humpbacks as follows:- Cook Strait, New Zealand 1922; Great Barrier Island, New Zealand 264; Tonga 84; (data and gonads collected by the writer and field collaborators); Albany, West Australia 699; Carnarvon, West Australia 5889; Point Cloates, West Australia 3321; Byron Bay, New South Wales 1040; Moreton Island, Queensland 6206; Norfolk Island 880; Durban, Natal 854; Madagascar, pelagic 2014; Congo 4071; (data provided on microfilm by Mr E. Vangstein, Sandefjord with the permission of the managers of the respective whaling companies. Valuable supplementary data on Australian catches was provided by Dr R.G. Chittleborough). Pre-war data includes 14,515 humpbacks as follows:- Coast of Natal 2621; Madagascar 1223; Western Australia land station 3426; Western Australia, pelagic 7244. Professor J.T. Ruud provided the pre-war records together with summarising tables and graphs prepared by himself and collaborators.

Antarctic catches in post-war years include 9857 humpbacks taken in late December and early February. In the 1932/33 to 1938/39 seasons, catching in Antarctic waters occurred from early November to late March, and data on 12,985 humpbacks caught between 65°S and 66°S have been obtained from Mr E. Vangstein who provided duplicate I.B.M. cards for each animal. Shore whaling in subantarctic waters has, in recent years, been confined to South Georgia where humpbacks have formed a negligible part of the catch. There were substantial catches earlier from South Georgia and other coastal waters of the Falkland Islands Dependencies and records exist for those caught between 1910 and 1917. These data are lodged in the British Museum (Nat. Hist.) where Dr F.C. Fraser kindly allowed me to examine them. South American humpback catches have been small and secondary to those of other species, so they have not been included in the present study.

**METHODS.** Gonads and other material and data obtained in New Zealand and Tonga were sufficient to classify the local catches in a number of ways that could be tested for statistically significant differences. Subdivisions into sex, and size categories showed little difference in the date of peak density of small males compared with small females, but there were substantial and inconsistent differences between the dates of peak density of large males as compared with large females. Classification based on reproductive data showed little or no difference between the time sequence of immature males and immature females, but suggested that the timing of mature females could be related more closely to their stage of breeding than to their size. Females at the end of lactation, resting females and pregnant animals followed

different time sequences of which that followed by resting females was most similar to the time sequence of mature males (Dawbin, 1960).

Except for the specified pregnant females, data on the reproductive condition of humpbacks are listed rarely in catch returns. In New Zealand catches the ovaries from 611 females and testes weights of 630 males indicated that females became mature at 39'6" and males at 38'. Those from which gonads had not been obtained were therefore classified as mature or immature according to whether they were above or below these lengths. Mature females whose mammary glands gave evidence of recent activity and those recorded as accompanied by a 'yearling' were classified as being at the end of lactation. Pregnant females are easy to recognize during processing as the fetuses of northbound humpbacks are large at New Zealand latitudes. The remaining mature females include resting animals and almost certainly include some that were at the end of lactation but for which there is inadequate data to allocate them to this category.

From the large Australian catches, Chittleborough (1958) has examined numerous gonads and found a close correlation between length and state of maturity using 36'9" as mean length for maturation of males and 38'6" as mean length for females. These lengths have therefore been used in this study to classify Australian catches and in view of the large samples on which the criteria are based, they have also been applied to data from all regions beyond Australasia. Because of the slight discrepancy between the estimated maturation lengths in Australia and New Zealand, data from other regions have also been analysed on the New Zealand criteria and by arbitrarily varying the lengths from 37 to 39 feet for males and 38 to 40 feet for females. The results did not produce significant changes in the calculated time sequences so the original criteria on maturity have been retained in the present analysis.

Some separation of mature non-pregnant females into stages of lactation or resting has been possible only for certain Australian catches. Dr Chittleborough has kindly provided data from four seasons' catches in Western Australia relating the proportion of mature females whose mammary glands showed signs of recent activity to that of other non-pregnant mature females. The pre-war Western Australia catches made before the minimum size length of 35 feet was established, include many whales whose length indicates that they were almost certainly yearlings

travelling with mothers near or at the end of lactation. In other regions non-pregnant mature females have been classified as a mixed group including resting and unspecified animals (shown as R & U in tables) of which an unknown proportion would be in late lactation.

With the above reservations, catch data on each humpback was used to classify the animal as immature (male or female); mature male; lactating, resting, pregnant or unspecified mature female.

Catches from relatively fixed positions (land stations or coastal factory ships) were classified as above and then grouped for each category into weeks for each season. As differences between time sequences per season at any one locality proved non-significant, the data for successive seasons were pooled for each week as shown in the appended tables.

The weeks were specified starting from 1st May which is the earliest commencing date for the most southern shore station under consideration (Cook Strait, 41°S). To facilitate comparable analyses for each station, the weeks were arbitrarily numbered commencing from May 1 and the same week code system has been used for all non-polar whaling localities, i.e., May 1-7, May 8-12, May 13-21, 3, etc. The numbering for Antarctic catches commences with November 6-12, 1, etc.

From the weekly frequencies of each humpback category per locality, the mean date, standard deviation and 95% confidence limits of the mean were calculated. The limits used were two standard errors on either side of the mean for samples exceeding 30 and Yates correction in the few cases where samples have been smaller than 30. The results have been presented in the graphical form (with slight modifications) described by Hubbs and Hubbs (1953). In the present graphs (Figs 23 & 25) the mean date is indicated by a white line within the black area that represents the 95% confidence limits on either side. Range has been omitted since this is determined frequently by a lone early or late whale and is therefore not relevant to the main theme of this study.

As pointed out by Hubbs & Hubbs, considerable reliance can be placed on the significance of the difference between samples, if the corresponding rectangles (referring to the total range of four standard errors of the mean) are only slightly separated, or if the overlap is not more than about 33% of the length of the shorter of the two rectangles. An approximate idea of the significance of an observed difference can be ob-

tained by inspection of Fig. 4 in Hubbs and Hubbs. In all doubtful cases,  $t$  tests were applied to determine whether or not a difference was significant at the 5% level or less. Coded means have been reconverted to calendar dates in Tables 12, 14 & 19.

Antarctic pelagic catches have been subdivided firstly into groups according to latitude and secondly into sectors of longitude subdivided into latitudes before classification as above.

While the tables list the humpback groupings used in the analyses, the graphs for clarity show fortnightly groupings to avoid some of the weekly random fluctuations or the alternative of smoothing the data. Graphs of percentage composition per fortnight are included as a guide to the probable composition of catches concentrated into selected portions of the humpback season and as a comparison with earlier data which have been published in the form of percentage changes during the whaling season. It must be emphasised that such data are of very doubtful value if applied to the season as a whole. For example, Fig. 2 suggests a fairly continuous replacement of immature humpbacks by mature animals throughout the season, but Fig. 1 shows that this is the result of a relatively small time difference in the periods of peak density of immature compared with mature whales. Other figures illustrate many comparable cases.

The separation of northbound from southbound humpbacks has, in the absence of individual data on direction of travel, depended on sighting records of the proportion of all humpbacks travelling north or south during the migratory season. Sources of error in such data are discussed below. *Sampling Error.* Catches are not completely random samples of the populations from which they are drawn, and the main sources of sampling error are considered below.

a) *Size.* The minimum length of 35 feet specified by the International Whaling Commission in 1937 normally gives complete protection to the 'yearling' group that range from about 28 to 31 feet in length. Data on yearlings must therefore be obtained from catches made prior to 1937 or from sightings at sea. Members of this group are seen very frequently accompanying their mothers in higher temperate latitudes, but they usually become independent in the tropics.

A proportion of immature whales of other age groups included in the 30 to 35 feet length range, are also protected by the size regulation, but those between 35 feet and the size of sexual maturity can be caught. However, they are likely to be

under-represented due to gunner selection for whales of greater size. The degree to which this occurs has varied between stations and seasons due to changes in relative availability of larger whales, and the effects in some cases of operating under quotas. Within the group of immature whales which are caught, there is no known means of distinguishing the sexes at sea, so, as females reach a greater size than males before becoming sexually mature, they would be expected to form a higher proportion in the catch of immature whales than that in which they occur in the whole migrating population of immature whales.

Mature females grow to a greater maximum size than mature males and gunner selection for the largest whales would be expected to increase the relative representation of this group in the catch compared with the population as a whole. However, this effect is counterbalanced to varying degrees by the next factor.

b) *Presence of Calves.* Cows accompanied by suckling calves are given protection by the International Whaling regulations, and this protection is of greatest importance among southbound humpbacks returning from the breeding grounds, and among those in the Antarctic feeding grounds where the calves are still suckling. It is less important in the temperate zones where northbound calves are in the process of being weaned and are almost certainly capable of continuing their existence independently of the mother, so the mother is often hunted. However, some whalers have actively avoided the mothers of these weaning yearlings, and the difference in policy relative to this group has provided some marked differences in catch composition between stations.

c) *Pregnant Whales.* It is generally assumed that pregnant females cannot be identified as such at sea and no regulations relating to this class of whales have been made. However, the proportion of pregnant whales changes during the northward migration because of the birth of calves at various latitudes en route. Towards the end of northward movement a high proportion of females which were in late pregnancy when they left the Antarctic seas, have undergone parturition becoming recognizable as cows accompanied by young calves and they then receive full protection. By the time the southward migration commences all whales which had left the Antarctic in late pregnancy have delivered calves and, except for those which have lost their calves, this whole group is protected during their return migration and subsequent stay in Antarctic waters.



There is some evidence of an additional complicating factor in certain regions where whales close to parturition are encountered. At least one gunner (the Master gunner at Norfolk Island) has stated that he can recognize females in very late pregnancy by their slower movements and general behaviour, and he is therefore able to select against such animals. The lack of females in late pregnancy in Norfolk Island catches at periods when this group would be expected to pass the island, lends some support to his contention.

Another group of pregnant whales are those which are southbound shortly after conception in the tropics and consequently the foetuses are very small during the southward migration. There are relatively few tropical and temperate zone records of this group partly because the greater part of southern hemisphere shore whaling is concentrated on northbound animals and partly because the very early foetuses are difficult to find in the brief examination which is all that is possible at many shore stations.

d) Curtailment of Season. Catches in some regions have been restricted to limited parts of the humpback season by specifying dates between which catching is permitted or by imposing quotas which, when filled, close the season. Antarctic catches since 1949 have been made in periods ranging from four to fourteen days in any one season, so have been too short to demonstrate time sequences within a season. There is even some evidence that the three of four month catching periods between 1931 and 1939 were probably insufficient to sample adequately the sequence of humpbacks during arrival and departure from the feeding grounds.

Quotas setting the upper limit of catch were applied to all Australian whaling stations during post-war years. When humpbacks were abundant, the existence of quotas encouraged companies to delay whaling until there had been numerous sightings that would assure the gunners of regular catches with good opportunities of selecting large animals. The earliest humpbacks were therefore under-represented in catches. When quotas were filled quickly the late humpbacks were not sampled. In some cases catches sampled part only of the northbound stock and in other seasons part of the southbound as well as all but the earliest northbound whales were sampled.

e) Specification of northbound and southbound humpbacks. At whaling localities north of 30°S, there is some overlap between the last northbound humpbacks and the earliest southbound humpbacks, but the catch data do not specify the

direction followed by individuals caught. Fortunately there is some information giving the approximate dates on which equal proportions of humpbacks are sighted travelling north compared with others travelling south past each locality except Congo. The latter, however, is probably close to the tropical end point of migration of the local humpbacks. All humpbacks caught prior to the date on which equal proportions travel north and south are classified as northbound and those after it are classified as southbound. Some of the humpbacks that travel north late and some of those that travel south early are therefore allocated incorrectly.

f) Effects of Sampling Errors. The sampling errors due to size selection, protection of cows accompanied by calves and the changing proportions of pregnant animals during migration, change substantially the degree of representation of several humpback categories at various latitudes, but there is no evidence that it modifies significantly the mean dates calculated for the categories specified in this study. So long as the type of selection at any one station remains fairly constant throughout the season, the degree of under- or over-representation of each category should also remain relatively steady throughout the season. The effect of under-representation is a tendency to increase slightly the standard error of the mean rather than the position of the mean. Providing each category is homogeneous and represented by numbers adequate for analysis, catch samples appear to be a satisfactory guide to the time of migration past each locality.

The apparent migration times of heterogeneous groups are, however, changed whenever there is a difference in selection between groups contained within the complex. Catches of mature females for example can rarely, if ever, be subdivided completely into lactating, resting and pregnant categories. There is frequently a heterogeneous group which includes resting and an unknown but probably variable proportion of unspecified animals (R & U group in tables), that are selected differently within a single locality. Among northbound whales, R & U includes females near or at the end of lactation, resting females and negligible number of unrecognized pregnant animals.

Even at stations where the data and material allow classification of most mature females into lactating, resting or pregnant, it is reasonably certain that some recently lactating animals are unrecognized as such and are classified as resting. As lactating or recently lactating animals tend to

travel northwards earlier than other categories, the merging of some of these with resting animals displaces the apparent mean date forwards by an unknown amount. However, the displacement is presumably greatest when no separation of lactating and resting animals is possible, and least when a high proportion of lactating animals can be specified separately from resting females. This is further complicated by changes in status of some mature females with latitude and with the differences in gunner selection referred to in section (b) above. To indicate this diagrammatically in Fig. 23, confidence limits have been omitted in the case of mixed females, but calculated means and standard deviations are included to account for all specimens. The actual values obtained are retained for reference in Table 12. Values for those 'resting' females from which a high proportion of lactating animals could be separated are shown in Fig. 23, but the above reservations on the relative homogeneity of this group should be borne in mind.

The mixture of all categories of mature females in contrast to mature males has been used frequently in past comparisons and has been shown in Figs 1-22 as a dotted line. These figures suggest great variability in seasonal trends between localities, but examination of data on the subdivisions within all mature females shows that this apparent variability is largely the result of changes in the relative proportions of the subdivisions.

Among southbound mature females there is a mixed group that includes resting females and some in early pregnancy, but there is no evidence that gunner selection operates differently between the two categories at any one locality or between different localities. As the available data are insufficient to separate these categories, estimated values for the mixed group are included in Fig. 25 as well as Table 14, but the group is clearly not as homogeneous as any of the other southbound categories specified.

Any curtailment of season that delays catching until after some of the early humpbacks have passed the catching zone results in a calculated mean date that is late compared with mean date which would have been obtained if the early animals had been represented in the catch. Similarly, if the season ends before the last category of humpbacks has passed, the calculated mean date for the latter will be displaced forwards. Both early and late curtailment of the season therefore causes displacement towards the general mean of the total catch. Incorrect allocation of some individuals into northbound or south-

bound categories in cases of overlap between the two migrating streams also tends to minimize calculated differences between the timing of categories. Differences that nevertheless prove highly significant are likely to be real and to be greater than indicated in this study.

## RESULTS

The time sequence followed by specified categories of humpbacks as they travel to and from tropical breeding regions has been studied from samples obtained at a range of latitudes. Those in temperate and tropical waters have been considered first followed by an examination of those in Antarctic latitudes. The samples from temperate and tropical regions show no difference in trends between separate breeding stocks off west Africa, east Africa, west Australia and east of Australia so the coastal whaling localities have been considered in order of latitude from south to north (except for Tonga) regardless of longitude. This arrangement approximates the sequences in which lines of latitude are traversed by northbound humpbacks. These form the largest proportion of the catch sample at all temperate and tropical latitudes except at Tonga where southbound humpbacks only are caught. Catch samples from the latter have therefore been discussed after a consideration of those from other non-polar localities, followed by the results obtained from Antarctic waters.

### TEMPERATE AND TROPICAL WATERS

*Cook Strait, New Zealand, 41°S.* It has been shown previously (Dawbin, 1956) that catches in Cook Strait are taken almost exclusively from whales during one stage of migration, i.e. northbound towards the breeding areas. Southbound humpbacks pass through Cook Strait exceedingly rarely. Lookouts are posted at high vantage points some weeks before the humpbacks are expected to traverse Cook Strait, and catching commences immediately after the first few humpbacks have been seen. Operations continue until a week or more has passed without sighting a humpback. The catch, therefore, includes samples from start to end of the northward migration past Cook Strait, and the majority of those sighted have been caught.

The small boat catching methods and the days lost through bad weather ensures that gunners catch whales primarily through availability with little possibility of selection, except for rejection of the smallest whales.



TABLE 1. Weekly catches of specified humpbacks, 1947-1960. Cook Strait, NZ, 41°S.

Start of week	Immature		All immatures	Mature				All humpbacks
	%	#		%	Lact. ♀	R + U ♀	Preg ♀	
1/5		1	1					1
8/5	3	5	8		2			10
15/5	6	6	12	5	5	1		23
22/5	24	28	52	23	25	3		100
29/5	68	47	115	31	21	13	2	182
5/6	55	53	108	70	27	11	4	227
12/6	52	42	95	84	22	33	8	242
19/6	49	31	80	134	8	28	20	270
26/6	35	31	66	123	4	23	29	247
3/7	23	16	39	106	5	11	24	206
10/7	8	7	15	73	1	7	8	136
17/7	2	8	10	53		19	22	104
24/7	3	8	11	16		11	12	90
31/7	5	1	6	22		7	10	43
7/8				9		3	4	16
14/8				7		4	1	12
Total	336	264	620	802	120	216	164	1922

Samples have been obtained through the catches of each of the seasons 1947 to 1960 totalling 1922 humpbacks. This is supplemented by sighting data on others, including the highly significant group of weaning yearlings observed as accompanying their mothers.

Females in late lactation form the earliest category at Cook Strait (Figs 1-2, Table 1). Most have been caught before mid-June, and none later than mid-July in any of 14 seasons. During this period the size of the local humpback stock appears to have been fairly stable, so the number of females in late lactation (as defined above) should have been approximately the same as those in late pregnancy, except for a slight reduction caused by the natural mortality of some calves before weaning. The 120 recorded compares with 164 in late pregnancy, and suggests that a few in late lactation may have been unrecognised and grouped among the 216 recorded as resting and unspecified. However, no 'yearlings' accompanying their mothers have been observed after mid-July, so it seems probable that the time sequence indicated by the recorded females in late lactation is substantially correct.

Immature males and females (Table 1) show no significant difference in mean dates. They have

therefore been combined in Figs 1 and 2 which shows the number and percentage frequency per fortnight respectively. It is evident that largest numbers occur about one week later than late lactating females, and about two weeks earlier than those of mature males. Immature animals have been represented from the beginning of each season, but none have been caught during the final two weeks in any season. Percentage frequencies (Fig. 2) show that immature animals form a steadily decreasing proportion of the catch per fortnight as the season progresses, but Fig. 1 shows that this is the result of a relatively small time difference between the attainment of peak density by immature animals compared with the categories of mature humpbacks.

Mature males form the largest single category of humpbacks at Cook Strait. None have been caught before mid-May, but the group has been represented during the remainder of the season. Peak density occurs in late June with a mean date of June 29.

Resting females, including a few unspecified animals that may have been in late lactation, have followed a very similar time sequence to that of mature males. There is no significant difference in mean dates or duration of season between these categories, but there have been nearly four times as many mature males as resting females in the catch.

Females in late pregnancy have formed the last category in all seasons during which they have been represented. None have occurred in May and the mean date (July 8) is about one week later than those of mature males or resting females. Pregnant females are therefore approximately one month later than those in late lactation.

*Great Barrier Is., New Zealand 36°S.* As at Cook Strait, the humpback catches from waters near Great Barrier Island include a high proportion of all those sighted, and represent all categories except those of smallest sizes. The last north-bound humpbacks leave the area some five or six weeks before the return of the earliest southbound animals, so there is no difficulty in separating animals on direction of travel. Data with gonads and other material have been obtained during the three seasons 1959-1961 relating to 231 north-bound and 33 southbound animals, but the material does not include mammary gland samples or observations on yearlings accompanying their mothers. It is therefore impossible to specify females in late lactation.

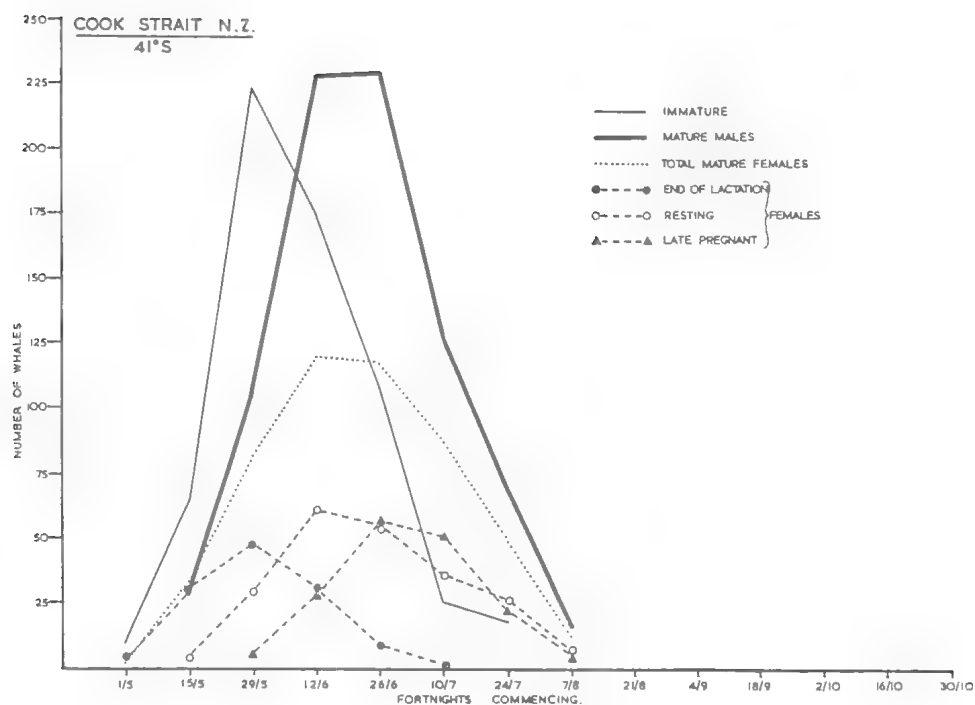


FIG. 1. Fortnightly catches of specified humpback categories, 1947-1960. Cook Strait, NZ, 41°S.

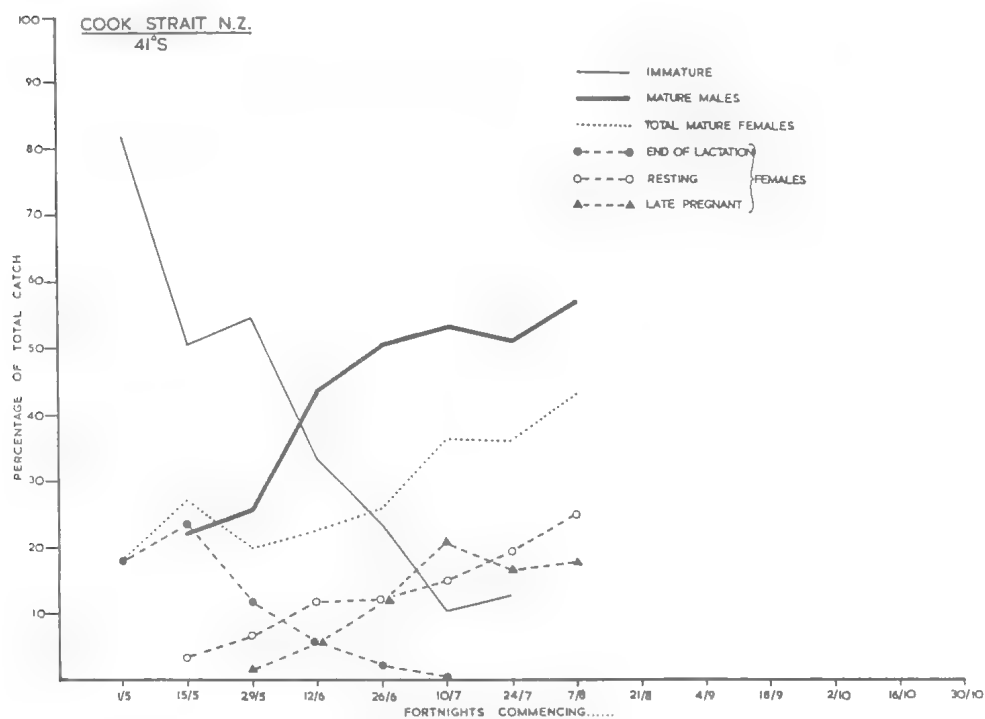


FIG. 2. Fortnightly percentages of specified humpback categories, 1947-1960. Cook Strait, NZ, 41°S.

TABLE 2. Weekly catches of specified humpbacks, 1959-1961. Great Barrier Island, NZ, 36°S.

Start of week	Immature		All immatures	Mature				All humpbacks
	♂	♀		♂	Lact. ♀	R + U ♀	Preg. ♀	
22/5	1		1	1				2
29/5	3	2	5	1		3		9
5/6	8	2	10	11		7		28
12/6	21	3	24	14		7		45
19/6	11	5	16	17		5	1	39
26/6	4	2	6	13		5	2	26
3/7	2	2	4	9		3	3	19
10/7	5	1	6	24		4	3	37
17/7		1	1	9		6	1	17
24/7				3			1	4
31/7				4		1		5
7/8								
14/8								
21/8								
28/8								
4/9								
11/9		2	2			2		4
18/9								
25/9	2	3	5			5		10
2/10								
9/10						2		2
16/10	1	2	3	1		2		6
23/10		2	2	4		4		10
30/10		1	1					1
Total	58	28	86	111		56	11	264

The earliest identifiable category comprises the immature animals (Figs 3-4, Table 2) which are represented in catches from the start of the season in late May until about mid-July, but none have been caught in the last two weeks of the northbound season. The mean date is 11 days earlier than that for mature males.

Mixed mature females include both resting and unspecified lactating females, and are represented throughout the season. The estimated mean date is mid-way between those for immature animals and mature males, so is relatively earlier than resting females at Cook Strait. This is almost certainly the result of including all the late lactating females, since this group elsewhere tends to travel earlier than other mature females.

Mature males form the largest group and are represented throughout the season. The mean date is 11 days after that of immature animals, and

TABLE 3. Weekly catches of specified humpbacks, 1952-1958. Albany, WA, 35°S.

Start of week	Immature		All immatures	Mature				All humpbacks
	♂	♀		♂	Lact. ♀	R + U ♀	Preg. ♀	
29/5	1	0	1	1	2		0	4
5/6	2	6	8	1	6	1	0	16
12/6	8	10	18	7	16	2	0	43
19/6	10	11	21	19	10	6	0	56
26/6	13	8	21	36	8	5	0	70
3/7	14	17	31	39	8	11	6	95
10/7	17	9	26	46	9	19	4	104
17/7	9	4	13	48	5	20	7	93
24/7	5	9	14	33	3	17	14	81
31/7	3	1	4	29	2	17	13	65
7/8	1	2	3	11		5	12	31
14/8	2	1	3	10		5	7	25
21/8	0	0	0	6		3	1	10
28/8	0	1	1	3		1	1	6
Total	85	79	164	289	69	112	65	699

8 days earlier than for pregnant females. Pregnant females form a small sample, but all were obtained after the first month of whaling, and the group was clearly the last northbound category.

Southbound humpbacks caught between mid-September and late October form a small sample in which there is no demonstrable difference in timing between mixed females and immature humpbacks, but the five mature males obtained were all caught after mid-October. (Fig. 25, Tables 2, 14).

Albany, WA, 35°S. The catch is taken from an exclusively northbound population, as humpbacks returning south from Western Australian coastal breeding areas follow a route some distance west of Albany. Although quotas have been applied in each season, catching has been carried on throughout most of the local humpback season before the quotas were filled. Except for protection of undersized whales, the Albany catch appears to be a representative sample of the local stock throughout its season of migration past the locality. Catching has commenced about three weeks later than at the higher latitude of Cook Strait. Catches in the seven seasons 1952-1958 include 699 humpbacks.

Females classified as at or recently in late lactation form the earliest category (Figs 5, 6, 23, Tables 3 and 14) with peak density in mid-June

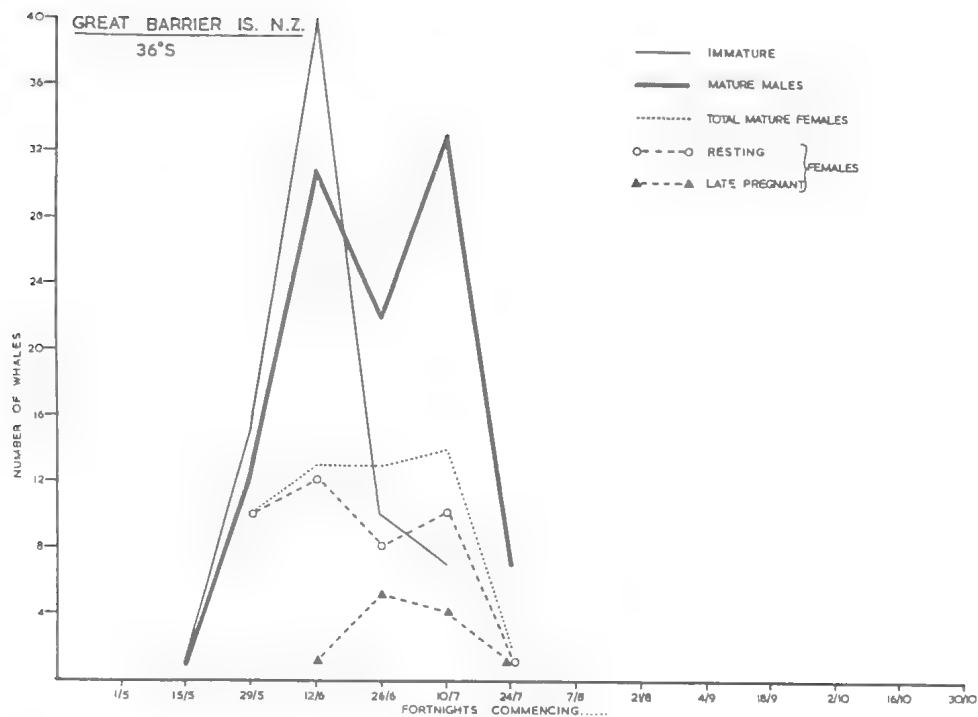


FIG. 3. Fortnightly catches of specified humpback categories, 1959-1961. Great Barrier Is., NZ, 36°S.

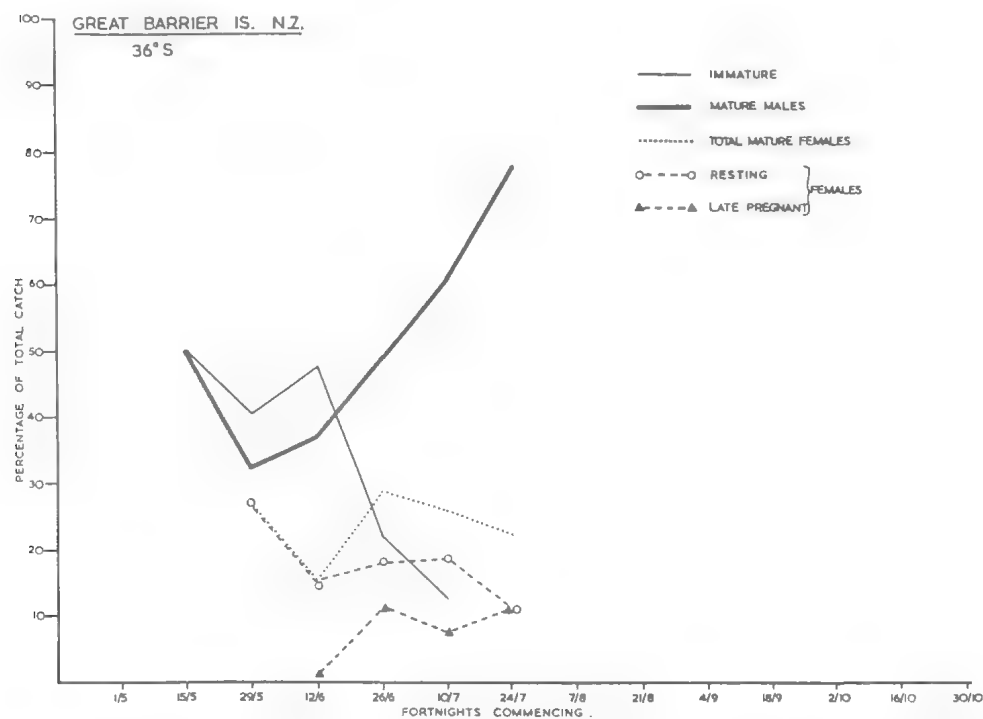


FIG. 4. Fortnightly percentages of specified humpback categories, 1959-1961. Great Barrier Is., NZ, 36°S.

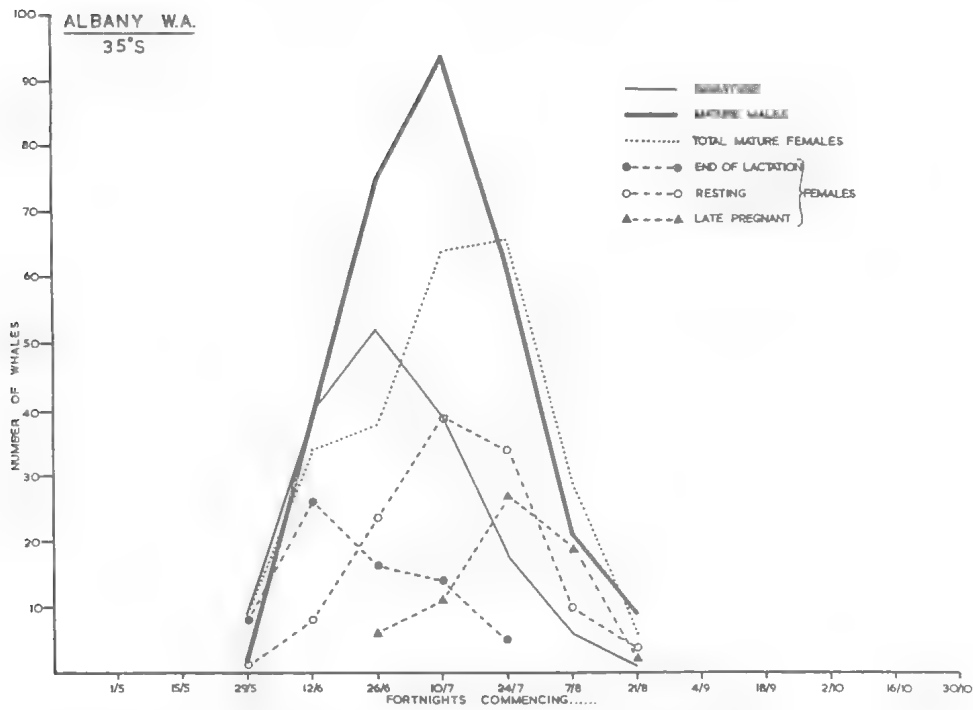


FIG. 5. Fortnightly catches of specified humpback categories, 1952-1958. Albany, WA, 35°S.

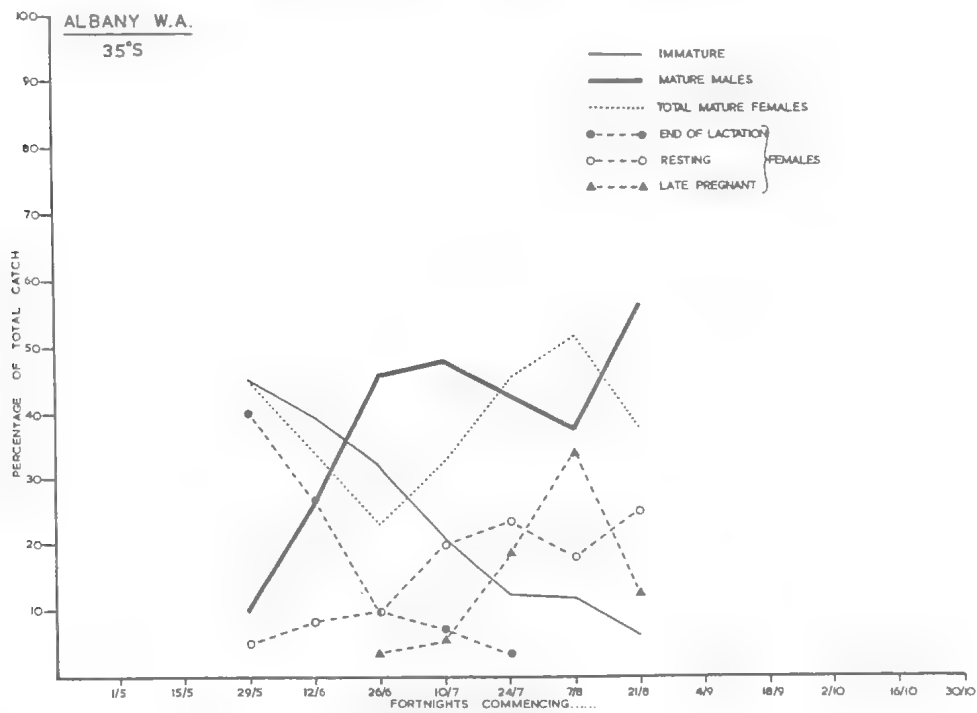


FIG. 6. Fortnightly percentages of specified humpback categories, 1952-1958. Albany, WA, 35°S.

TABLE 4. Weekly catches of specified humpbacks, 1948-1954. Durban, Natal, 30°S.

Start of week	Immature		All immatures	Mature				All humpbacks
	♂	♀		♂	Lact. ♀	R + U ♀	Preg. ♀	
15/5	0	1	1	0		0		1
22/5	2	0	2	0		0		2
29/5	5	2	7	1		1		9
5/6	3	5	8	6		6		20
12/6	10	13	23	10		4		37
19/6	21	17	38	20		12		70
26/6	28	37	65	31		15		111
3/7	22	24	46	42		15		103
10/7	18	20	38	37		15		90
17/7	14	23	37	24		21		82
24/7	14	16	30	29		16		75
31/7	7	12	19	6		10		35
7/8	7	6	13	4		5		22
14/8	2	3	5	2		3		10
21/8	6	8	14	6		4		24
28/8	2	10	12	2		2		16
4/9	0	0	0	2		1		3
11/9	3	2	5	5		5		15
18/9	11	12	23	13		10		46
25/9	12	12	24	19		7		50
2/10	1	5	6	7		6		19
9/10	3	1	4	4		3		11
16/10	0	0	0	1		0		1
23/10	0	0	0	1		0		1
30/10	0	0	0	1		0		1
Total	191	229	420	273		161		854

and none during the last four weeks of the season. The mean date (June 28) is about one week earlier than that of immature whales. The latter are represented throughout the season, but of 164 caught, seven only were caught during the last four weeks of the season. Mature males have also been caught through the season, but peak density occurred during July and the mean date was 10 days later than for immature whales. Resting and unspecified females had a time sequence similar to that of mature males. The small difference in mean dates is not significant.

Females in late pregnancy have not been recorded during the first five weeks of the season, and their mean date is about two weeks later than that of mature males. They have occurred one month later than late lactating females, and they

comprise the last category to migrate northwards past Albany.

*Durban, Natal 30°S.* Humpback catches from Durban during post-war years have differed from those made near any of the other temperate and tropical localities under consideration in being secondary to catches of other species. Sperm and fin whales have formed the major part of the catch, and both of these species tend to occur at a greater distance from shore than most humpbacks. While the writer has no personal knowledge of the local conditions, the total catch composition suggests that humpbacks are caught as opportunity arises between catches of the more valuable and intensively sought sperm and fin whales, so the humpback catch is possibly not a consistent sample of the locally migrating stock.

The composition of humpback catches is unusual in the very high proportion of immature animals, which on the present criteria represent nearly half the total catch, and on the criteria used in International Whaling Statistics they form about two thirds of the total catch. The absence of foetus records suggests that pregnant females traverse waters closer to shore or further out to sea than the main catching zone, or that the data on pregnant females is incomplete. The overall low percentage of mature females shows that incomplete recording cannot be the full explanation, and may not even be part explanation.

The writer has no substantial data on which to separate northbound from southbound animals, but the bimodal peaks in the present and Matthews (1937) data indicate that the change occurs during August. Trial analyses were carried out on data from the start of season to August 13, August 20, August 27 and September 3, with little difference in sequence resulting. Mid-August (actually up to August 13) has been used in the calculations shown in Table 12 & Fig. 23. The post-war data relates to 854 humpbacks caught during the 1948-1954 seasons, and includes 667 which have been classified as northbound.

Immature whales form the earliest identifiable category, followed by mature males, then mixed females, but the time intervals between the mean dates of these categories (Table 12) are too small to be significant at the 5% level.

Pre-war catches generally included a higher proportion of humpbacks than other species, so they are likely to be a more representative sample of the local humpback stock. Catches by one company at Durban in 1934 and 1935 included 547 that have been classified as northbound since

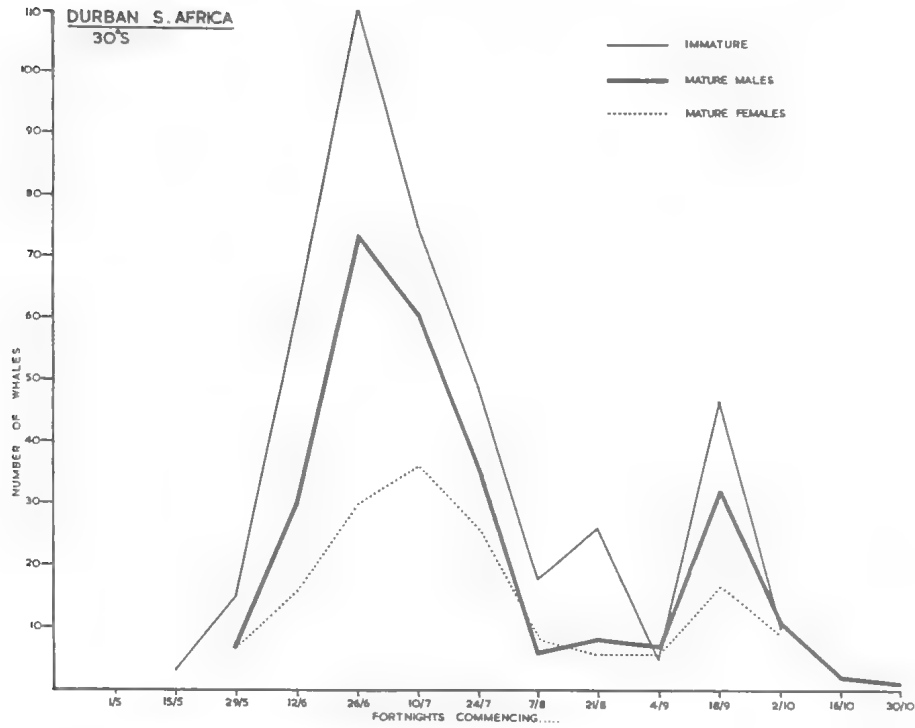


FIG. 7. Fortnightly catches of specified humpback categories, 1948-1954. Durban, Natal, 30°S.

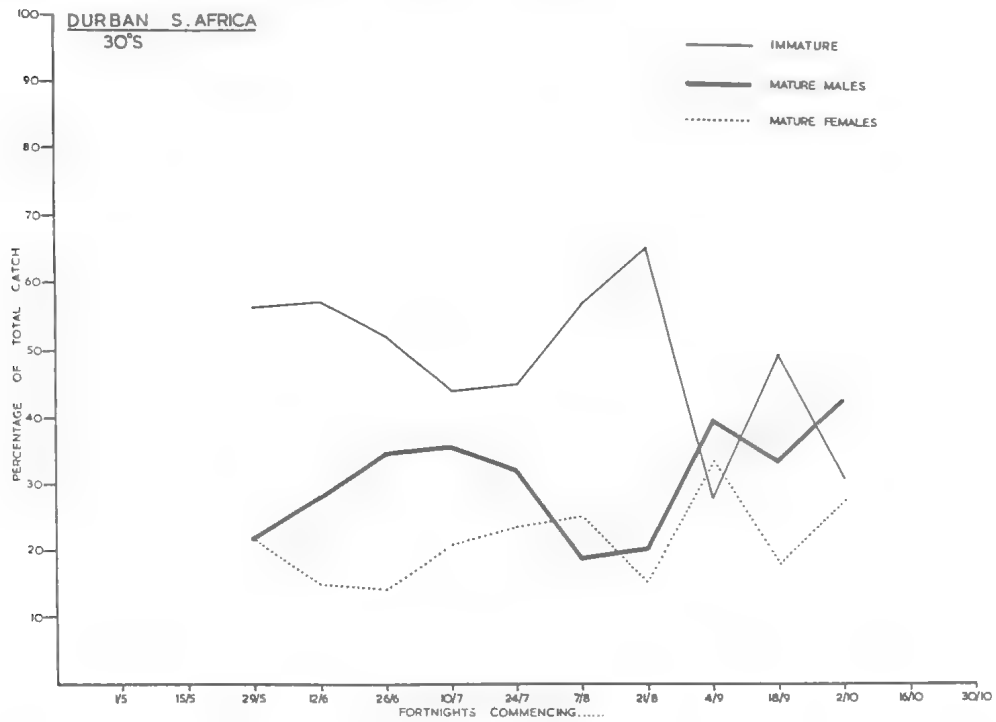


FIG. 8. Fortnightly percentages of specified humpback categories, 1948-1954. Durban, Natal, 30°S.



TABLE 5. Weekly catches of specified humpbacks, 1954-1961. Byron Bay, E Australia, 29°S.

Start of week	Immature		All immatures	Mature				All humpbacks
	♂	♀		♂	Lact. ♀	R + U ♀	Preg. ♀	
22/5				3				3
29/5				6		1		7
5/6	3	3	6	21		7		34
12/6	1	3	4	25		12		41
19/6	3	3	6	46		15	1	68
26/6	3	1	4	44		18	1	67
3/7	1	4	5	76		17	3	101
10/7	2	1	3	52		29	7	91
17/7	1	1	2	63		35	3	103
24/7		2	2	37		27	8	74
31/7		1	1	17		16	6	40
7/8	1	4	5	15		13	3	36
14/8		1	1	9		14		24
21/8	3	7	10	10		31	1	52
28/8	3	1	4	19		18		41
3/9	2	4	6	26		26		58
10/9	10	6	16	25		13	1	55
17/9	4	3	7	30		8	1	46
24/9	4	3	7	19		1		27
2/10		1	1	21				22
9/10	1	3	4	17		2		23
16/10	2		2	16				18
Total	44	52	96	605		304	35	1040

they were caught prior to mid-August. Among these, the order of appearance was the same as in post-war years, but the differences in mean dates were larger and were very highly significant. During the three weeks from mid-May into early June, immature animals only were caught. The mean date for immature whales (July 6) was 8 days earlier than for mature males, and two weeks earlier than for mixed females, but there are no data on which to subdivide the latter into lactating, resting and pregnant.

There are bimodal fluctuations within the post-war catches of southbound humpbacks (i.e., after mid-August) (Table 4, Figs 7-8) that cannot be explained by the writer. However, the pre-war catch sample from Durban in 1934 and 1935 was unimodal, and showed that immature whales precede mature males and mixed females on the southward migration.

TABLE 6. Weekly catches of specified humpbacks, 1956-1961. Norfolk Island, 29°S.

Start of week	Immature		All immatures	Mature				All humpbacks
	♂	♀		♂	Lact. ♀	R + U ♀	Preg. ♀	
5/6				2		1		3
12/6	1		1	2		2		5
19/6	1		1	13		1		15
26/6	4		4	30		7		41
3/7	6	1	7	35		10		52
10/7	10	2	12	39		8		59
17/7	4		4	30		2		36
24/7	4	6	10	25		7		42
31/7	2	2	4	36		12		52
7/8	5	1	6	27		9		42
14/8	1	4	5	14		12		31
21/8	1		1	10		9		20
28/8	2	3	5	19		19		43
4/9	5	2	7	5		20		32
11/9	3	15	18	12		40		70
18/9	5	4	9	12		37		58
25/9	6	9	15	21		20		56
2/10	5	4	9	58		17		84
9/10	2	1	3	44		16		63
16/10		2	2	24		3		29
23/10	2		2	29		6		37
30/10	1		1	8		1		10
Total	70	56	126	495		259		880

Byron Bay, EA 29°S, Norfolk Island, 29°S, Moreton Island, EA 27°S. Catch samples from stations of eastern Australia and Norfolk Island have shared substantial similarities due to quotas and selection factors in common. The samples used for analysis include the following seasons and catches:- Byron Bay 1954-1961, 1040; Norfolk Island 1956-1961, 880; Moreton Island 1952-1961, 6205. Although variations in the size of catch at each locality tend to mask some of the similarities (Figs 9, 11, 13), the changes in percentage composition per fortnight at each are strikingly similar (Figs 10, 12, 14).

At each locality, the quotas during most of the seasons considered in this study were markedly smaller than the number of humpbacks sighted. This has made it possible for gunners to select more stringently than occurs at localities where there is only a small excess of sightings compared to catch.

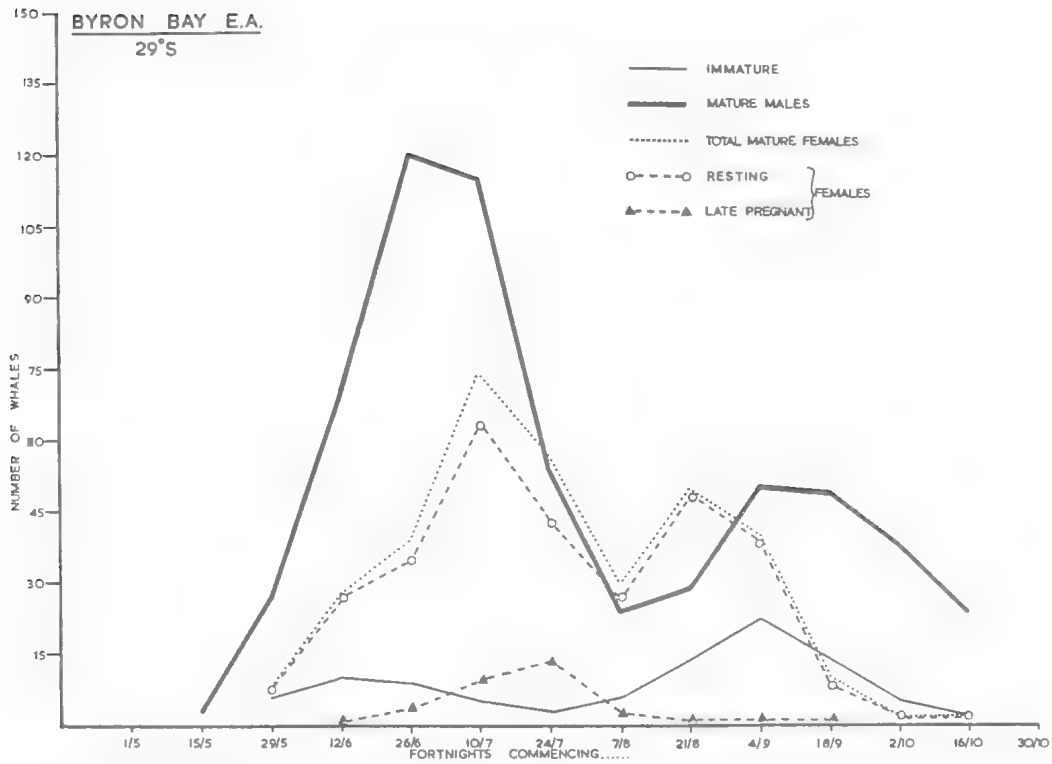


FIG. 9. Fortnightly catches of specified humpback categories, 1954-1961. Byron Bay, E Australia, 29°S.

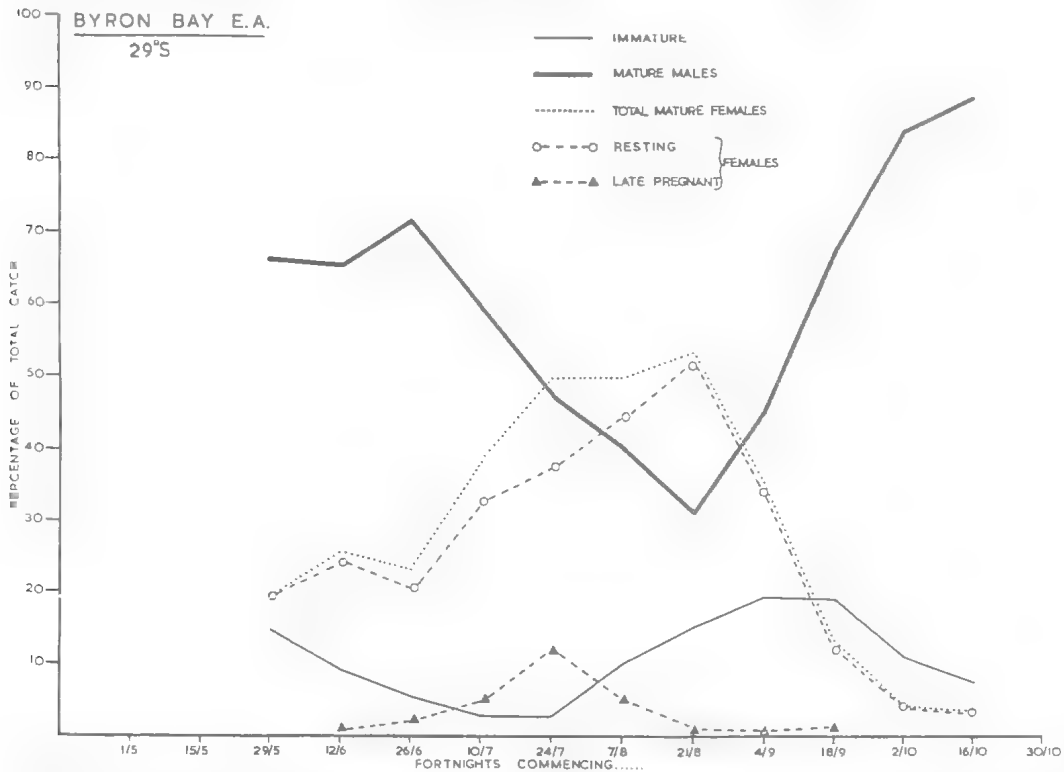


FIG. 10. Fortnightly percentages of specified humpback categories, 1954-1961. Byron Bay, E Australia, 29°S.

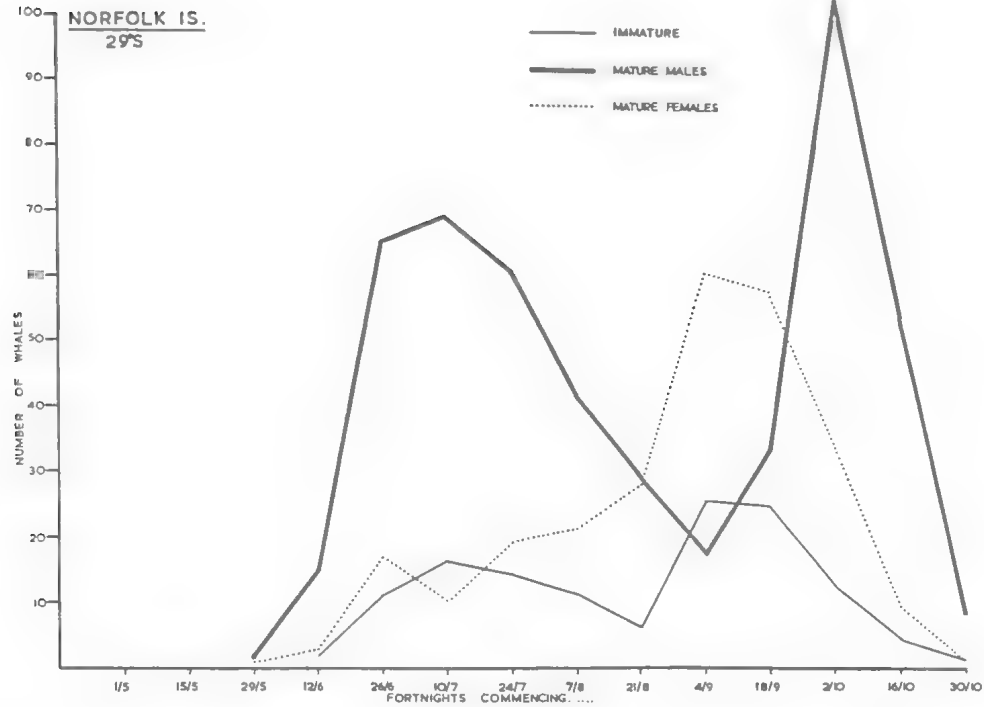


FIG. 11. Fortnightly catches of specified humpback categories, 1956-1961. Norfolk Is., 29°S.

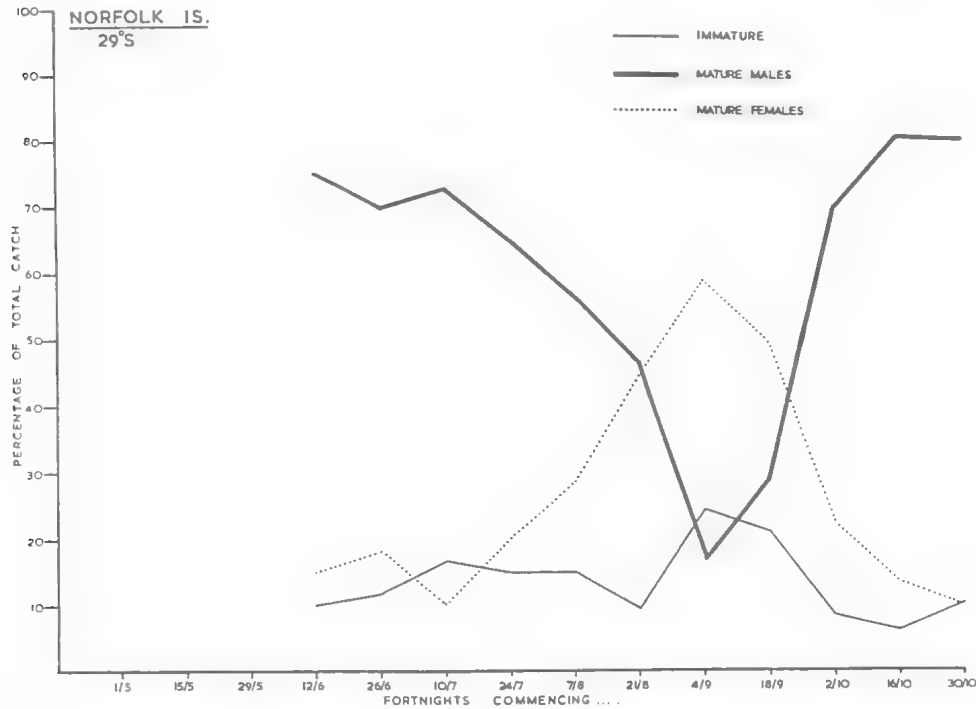


FIG. 12. Fortnightly percentages of specified humpback categories, 1956-1961. Norfolk Is., 29°S.

TABLE 7. Weekly catches of specified humpbacks, 1952-1961. Moreton Island, E Australia, 27°S.

Start of week	Immature		All immatures	Mature				All humpbacks
	♂	♀		♂	Lact. ♀	R + U ♀	Preg. ♀	
15/5				2				2
22/5				16				16
29/5	1	5	6	24		6		36
5/6	14	5	19	131		38	2	190
12/6	30	30	60	336		95		491
19/6	40	41	81	354		102	3	540
26/6	41	51	92	408		118	4	601
3/7	30	26	56	423		121	4	604
10/7	30	24	54	408		105	9	576
17/7	21	26	47	412		114	23	601
24/7	18	24	42	344		119	38	543
31/7	14	36	50	285		161	33	529
7/8	14	55	69	147		106	11	308
14/8	16	19	35	82		76	4	177
21/8	29	31	60	83		45	8	196
28/8	21	29	50	81		43	1	175
4/9	18	25	43	93		57		179
11/9	11	20	32	87		29	1	149
18/9	15	8	23	44		8		75
25/9	11	14	25	65		12	1	103
2/10	6	5	11	57		3		71
9/10	2	2	4	10		4		18
16/10	1		1	13		2		16
23/10				6				6
Total	384	436	820	3892		1347	146	6205

From each station, it has been the practice to avoid adults accompanied by yearlings, whether or not the adults may have been females which were at the point of weaning offspring capable of independent existence. Late lactating females have therefore been largely absent from catch samples.

Selection for size has been intense, especially during the early part of each season when gunners are usually hopeful of fulfilling the quota from large whales only. From each station, the whales caught during the earliest one or two weeks of the season have all been mature. Among the total catch of northbound humpbacks, the percentage of immature animals caught has been about one quarter of that at non-quota localities in the southern hemisphere (6, 12 & 11 for the former, 25-50 for the latter).

Since there is some indication that the under-representation of immature animals changes within each season according to the whalers' assessment of progress in filling the quotas, the available catch data may be a misleading sample of the local time sequence for immature whales. The calculated mean dates at each locality (Fig. 23, Table 12) show no significant differences from those of mature males. The latter are consistently earlier than mixed mature females which, due to selection against late lactating females, are mainly 'resting' animals.

Pregnant females are unrepresented in catches from Norfolk Island, but at Byron Bay and Moreton Island they form the last northbound category. The mean dates are approximately two weeks later than those for mature males at both localities.

Humpbacks classified as southbound have included those caught after August 21 at Byron Bay and Moreton Island, and after September 4 at Norfolk Island, since equal proportions of northbound and southbound whales were sighted at the respective localities on these dates.

Mixed females (early pregnant and resting) form the earliest southbound category at each locality, but the differences in time in relation to immature whales is non-significant, except at Byron Bay (Fig. 25, Table 14). Mature males are later than immature whales by amounts which are highly significant in each locality (Moreton Is., 5 days; Byron Bay, 8 days; Norfolk Is., 14 days). Females in early lactation are unrepresented in catches, but Chittleborough (1962) has shown that this category is the last to travel south along the coast of eastern Australia.

*Carnarvon, WA 25°S, Point Cloates, WA 22°S.* At both these stations the quotas per season were larger than those for Byron Bay, Moreton Island and Norfolk Island. The catch samples to be discussed here include Carnarvon 1950-1958, 5889, and Point Cloates 1949-1955, 3321. Catching at the latter locality ceased after the 1955 season. The length frequencies of catches indicates that gunner selection was usually less intense than at the latter stations and the catch samples used (1950-1958 at Carnarvon and 1949-1955 at Point Cloates) appear to be representative of the northbound population, except for humpbacks under 35 feet in length (Figs 15-18, Tables 8-9). The sample classified as northbound includes all those caught before August 28 at Carnarvon and August 21 at Point Cloates (Chittleborough, 1953).

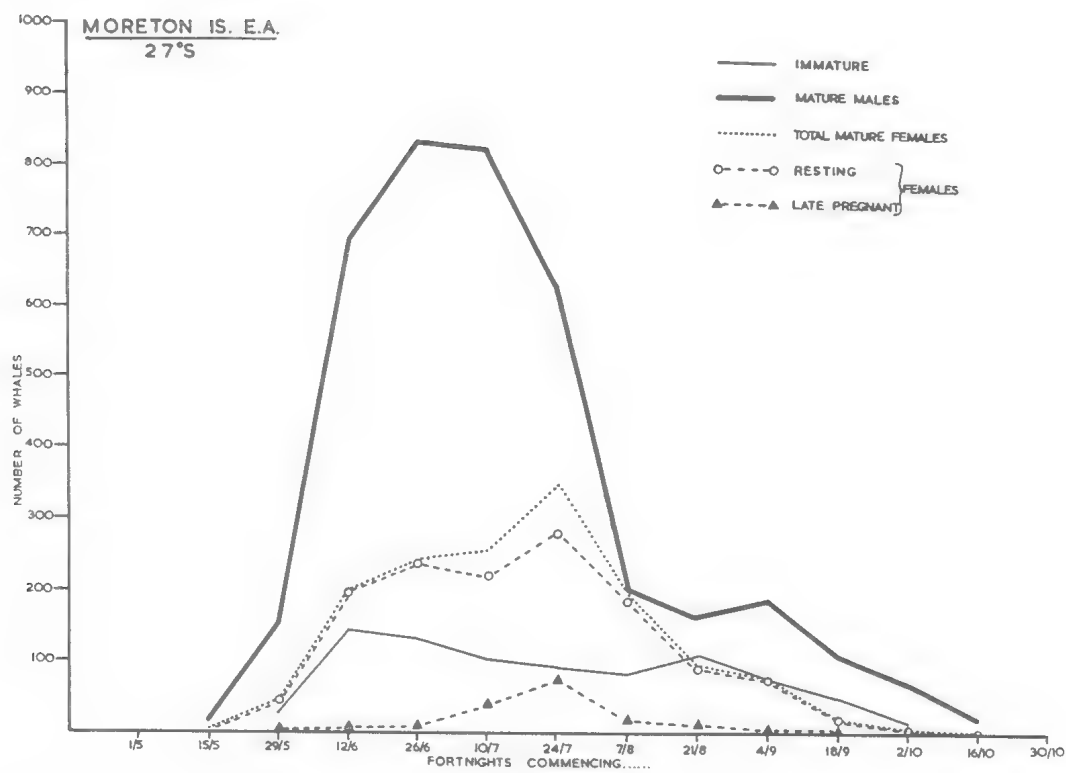


FIG. 13. Fortnightly catches of specified humpback categories, 1952-1961. Moreton Is., E Australia, 27°S.

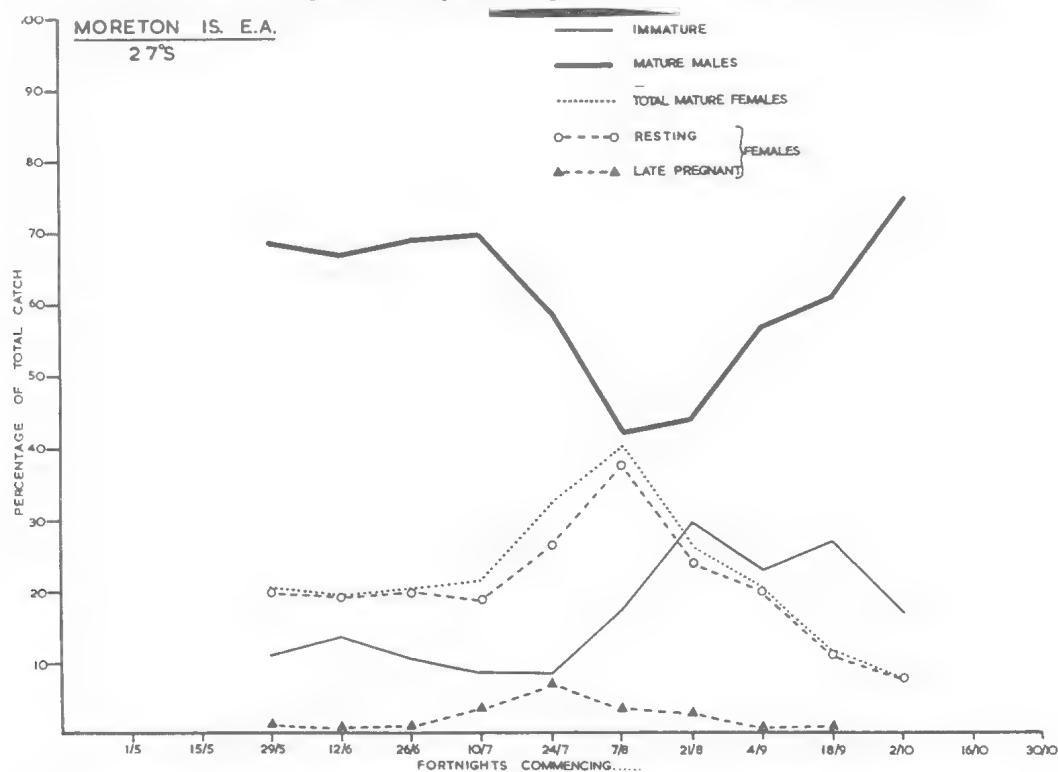


FIG. 14. Fortnightly percentages of specified humpback categories, 1952-1961. Moreton Is., E Australia, 27°S.

TABLE 8. Weekly catches of specified humpbacks, 1950-1958. Carnarvon, WA, 25°S.

Start of week	Immature		All immatures	Mature				All humpbacks
	♂	♀		♂	Lact. ♀	R + U ♀	Preg. ♀	
29/5	1	2	3	2	8	0	0	13
5/6	5	8	13	9	42	4	0	68
12/6	14	24	38	60	95	11	3	207
19/6	30	17	47	61	97	47	2	254
26/6	26	31	57	139	94	55	1	346
3/7	40	43	83	175	67	92	6	423
10/7	35	47	82	186	49	133	5	455
17/7	27	25	52	208	33	133	2	428
24/7	20	27	47	237	23	138	2	447
31/7	28	30	58	272	15	134	5	484
7/8	31	21	52	289	0	138	13	492
14/8	23	31	54	293	0	104	15	466
21/8	36	14	50	278	0	98	14	440
28/8	24	14	38	255	0	81	11	385
4/9	17	7	24	186	0	61	10	281
11/9	9	6	15	200	0	63	4	282
18/9	9	6	15	159	0	23	5	202
25/9	3	2	5	62	0	9	0	76
2/10	2	2	4	63	0	11	0	78
9/10	0	0	0	18	0	3	0	21
16/10	0	0	0	15	0	2	0	17
23/10	0	0	0	22	0	1	0	23
30/10	0	0	0	1	0	0	0	1
Total	380	357	737	3190	523	1341	98	5889

The number of females at the end of lactation have been calculated from mammary gland data kindly provided by Dr R.G. Chittleborough. Lactating females form the earliest category with mean dates (Fig. 23, Table 12) at Carnarvon 20 days and at Point Cloates 11 days prior to those for immature animals. The latter are 10 and 8 days earlier than the mean dates for mature males. The above time intervals are all very highly significant, but there is no significant difference between the mean dates for mature males and resting females.

Pregnant females form the last northbound group with mean dates 6 and 4 days later than mature males and about one month later than females at the end of lactation.

Catches off Western Australia during 1925-1928 were taken without quotas or length restrictions and therefore include a considerable number of the small size classes that are absent

TABLE 9. Weekly catches of specified humpbacks, 1949-1955. Point Cloates, WA, 22°S.

Start of week	Immature		All immatures	Mature				All humpbacks
	♂	♀		♂	Lact. ♀	R + U ♀	Preg. ♀	
5/6	0	0	0	0	1	0	0	1
12/6	0	1	1	0	11	1	1	14
19/6	5	18	23	12	21	2	0	58
26/6	17	24	41	26	25	12	8	112
3/7	22	38	60	68	38	23	15	204
10/7	13	21	34	74	25	34	16	183
17/7	24	60	84	123	23	63	12	305
24/7	20	27	47	130	14	58	20	269
31/7	17	32	49	157	11	67	20	304
7/8	18	27	45	170	7	61	21	304
14/8	7	25	32	110	0	54	19	215
21/8	26	33	59	143	0	74	12	288
28/8	25	42	67	115	0	95	9	286
4/9	22	35	57	132	0	78	3	270
11/9	18	22	40	103	0	58	1	202
18/9	5	13	18	71	0	25	1	115
25/9	4	3	7	70	0	24	1	102
2/10	1	2	3	57	0	15	0	75
9/10	0	0	0	12	0	2	0	14
Total	244	423	667	1573	176	746	159	3321

from post-war catches. Those of less than 30ft in length are of special interest, since they form the size classes represented among weaning 'yearlings'. In a total catch of 3,426 there were 174 examples occurring as follows:- 10 in June, 115 in July, and 49 in August. This represented 21%, 13% and 4% of the catch in these months and the 'yearlings' were clearly the earliest homogeneous group to pass the locality. Subsequent data have shown that most yearlings accompany the mother during the major part of the northward migration. Although the individual females cannot be specified from the data obtained during the above seasons, the time sequence of the yearlings is completely consistent with the occurrence of late lactating females as the earliest category in post-war catches. Immature animals (excluding yearlings) were the next group followed by mature males and mixed females. There are no data on pregnant animals. Thus all the categories which can be recognised in the 1925-1928 catches are consistent in time sequence with those in the 1949-1958 catches.

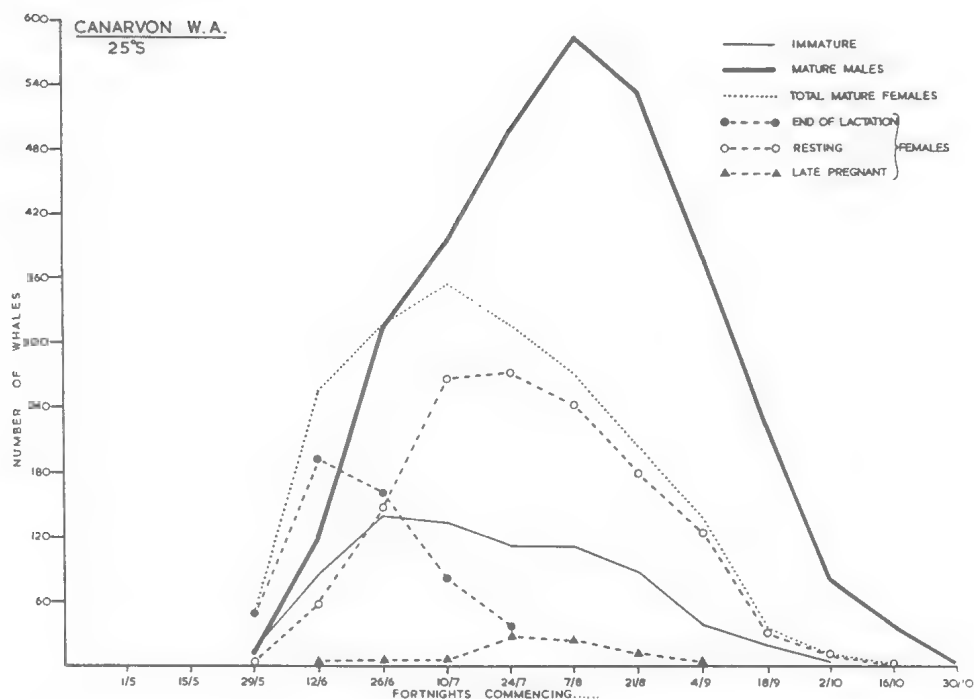


FIG. 15. Fortnightly catches of specified humpback categories, 1950-1958. Carnarvon, WA, 25°S.

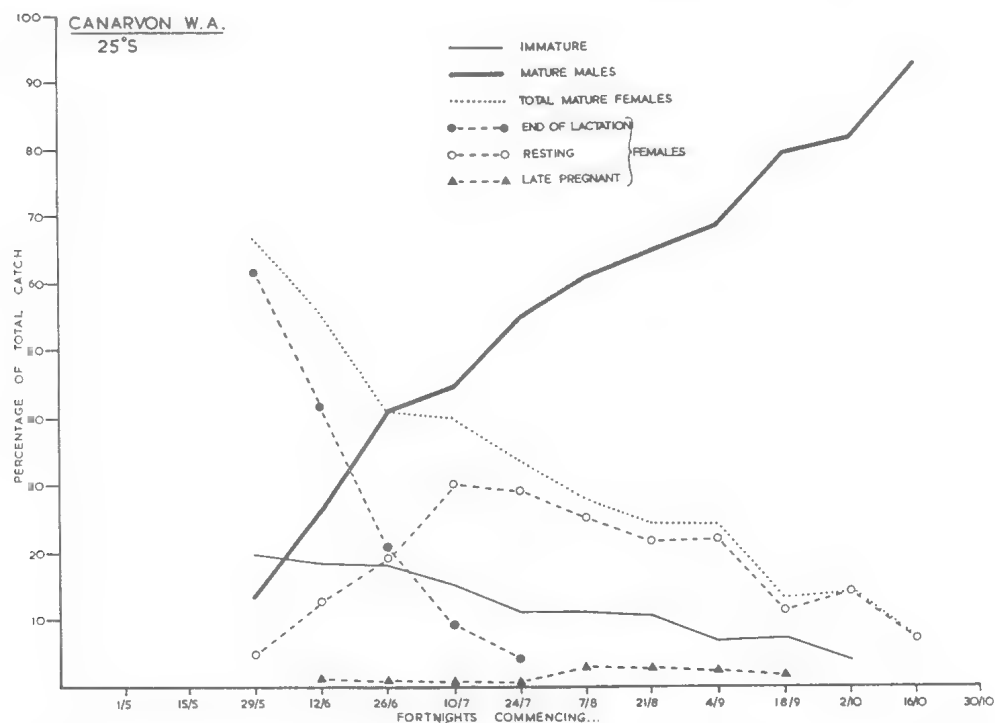


FIG. 16. Fortnightly percentages of specified humpback categories, 1950-1958. Carnarvon, WA, 25°S.



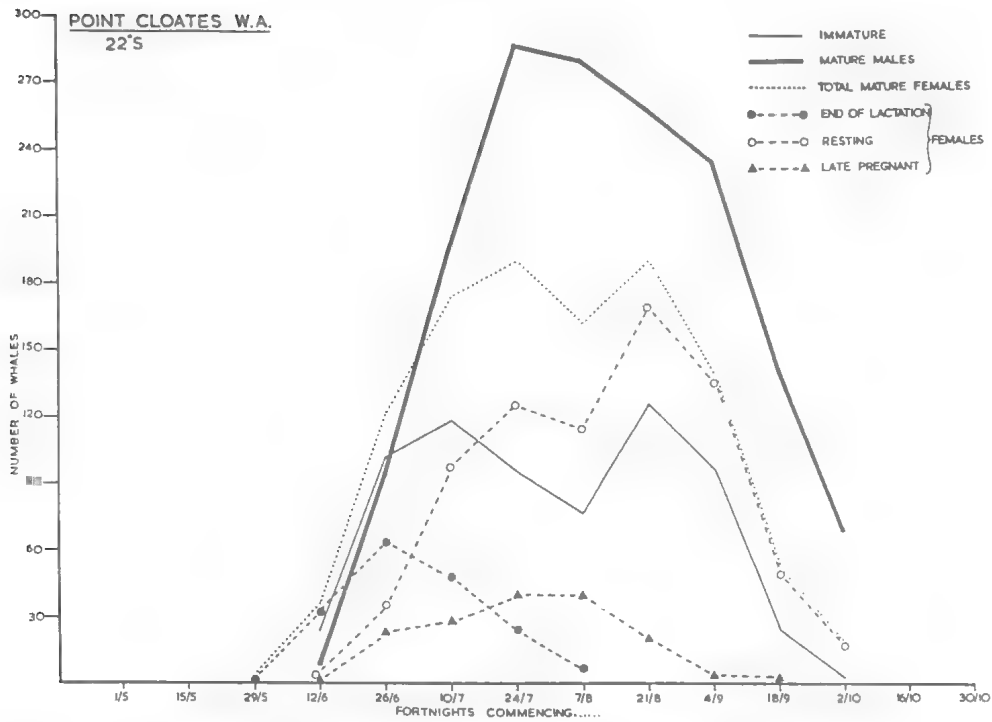


FIG. 17. Fortnightly catches of specified humpback categories, 1949-1955, Point Cloates, WA, 22°S.

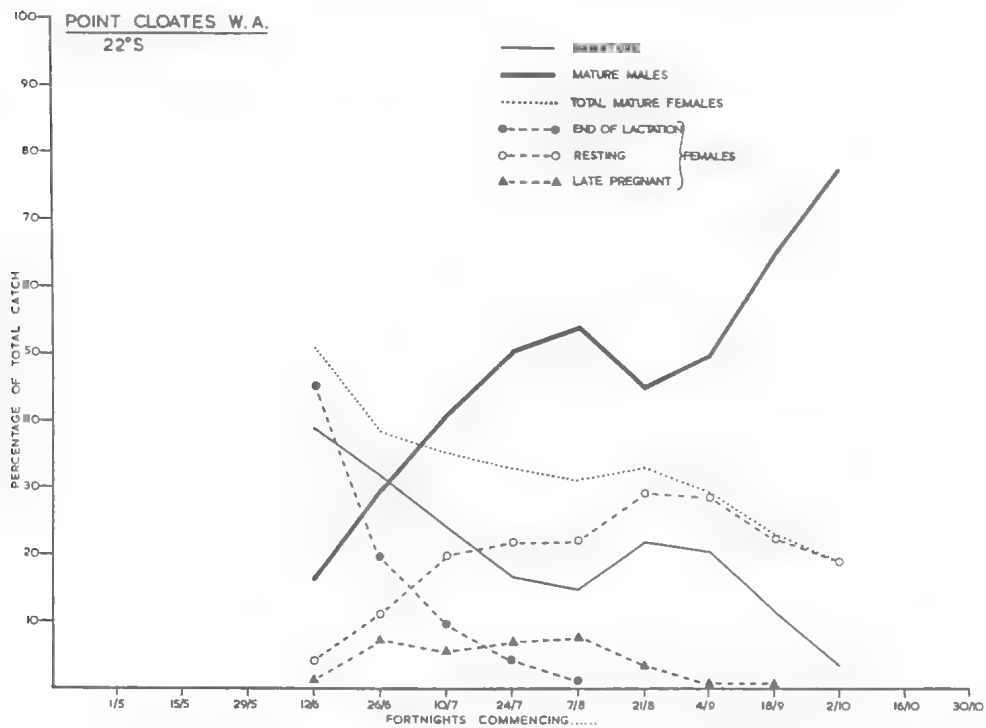


FIG. 18. Fortnightly percentages of specified humpback categories, 1949-1955, Point Cloates, WA, 22°S.

During the southward migration, immature animals have been the earliest recognisable category to travel past Western Australian land stations, while aerial observations by Chittleborough (1953) have shown that cows accompanied by young calves comprise the last group.

*Madagascar, Pelagic, 16°-26°S.* The catches from the coastal waters of Madagascar have been made by catchers operating with a factory ship that moved between 26°S & 16°S with 22°S as modal position. Irregularities of movement through this distance may have had some effects on catch composition, but there are no data indicating selection apart from rejection of under-sized whales. There are no data on which to specify lactating females. The catch in 1948 and 1949 totalled 2014 humpbacks (Table 10, Figs 19-20) of which 1819 caught before September 11 have been classified as northbound. This date has been derived from descriptions of the above seasons by Angot (1951).

Immature animals form the earliest recognisable category to the extent that they occur in approximately equal numbers to those of mature males between mid-June and mid-July, but occur in smaller numbers than mature males during the remainder of the season. This results in a calculated mean date of July 28 (Table 12, Fig. 23) for immature animals compared with July 31 for mature males. While this interval of 3 days is small, it is nevertheless significant at the 1% level. Mixed females, including unspecified late lactating and resting animals show no significant difference in timing compared with mature males.

Pregnant females have a mean date 16 days later than mature males and are the last northbound category.

The catches of southbound humpbacks (i.e., after September 11) were made during 3 to 4 weeks only. This period is insufficient to establish the time sequence of southbound animals passing Madagascar.

*Congo, 1°S.* There is little difference in latitude between Gabon and São Tomé Is. and the writer is unaware of significant differences in selection at the two localities. Catches have therefore been pooled under the heading 'Congo', and amount to 4,071 humpbacks taken during 1949 to 1952 (Figs 21-22, Table 11). As in the other post-war catches, animals under 35 feet in length are rarely represented. There are no data which can be used to specify animals that have been lactating re-

cently, so mature females include a mixture of the above and resting animals. Most females that were in late pregnancy when at higher latitudes have delivered their calves and became protected as cows accompanied by young calves before reaching 1°S. The catch of animals in late pregnancy has therefore been very small.

The Congo region is at or near the northern limit of the west African southern hemisphere humpbacks, so there is no clearly recognisable passage of northbound and southbound animals past the locality. Many specimens presumably remain for some weeks in the general breeding area before departing southwards, and there are no data on which to separate northbound from southbound animals. The total catch per season has therefore been used to calculate mean dates which, in these cases, represent the approximate mid-point between the beginning of northbound arrivals and the end of southbound departures for each category. This gives an earlier date for animals in late pregnancy relative to other categories since the former includes only northbound animals.

Immature animals form the earliest category (Figs 21-23) with the mean date on July 29 as compared with August 11 for mature males and mixed females (Table 12). Females in late pregnancy occur 10 days later on mean dates, and form the last category despite the non-representation of their southbound equivalents, (i.e., cows accompanied by young calves).

*Tonga, 22°S.* Unlike catches from all the preceding localities, those from Tonga have been taken predominantly from southbound animals, (Fig. 24, Table 13). The local whalers still use open boats, hand harpoons and hand lances, and with this equipment they concentrate, like many nineteenth century whalers with similar gear, on cows accompanied by young calves. This category is protected elsewhere by International Whaling regulations, and is unrepresented in other catches. While the catch from Tonga is small (82 in 5 years) it is nevertheless of special interest.

Hunting commences when cows with calves are first sighted, and these, together with immature whales up to about 38 feet, comprise the subsequent catch. However, observations at Foveaux Strait, NZ, and along both west and east coasts of Australia indicate that cows and calves form the last southbound group.

The delay in hunting until cows and calves appear makes it highly probable that early southbound immature whales will be unrepresented in the catch. Nevertheless, the immature whales

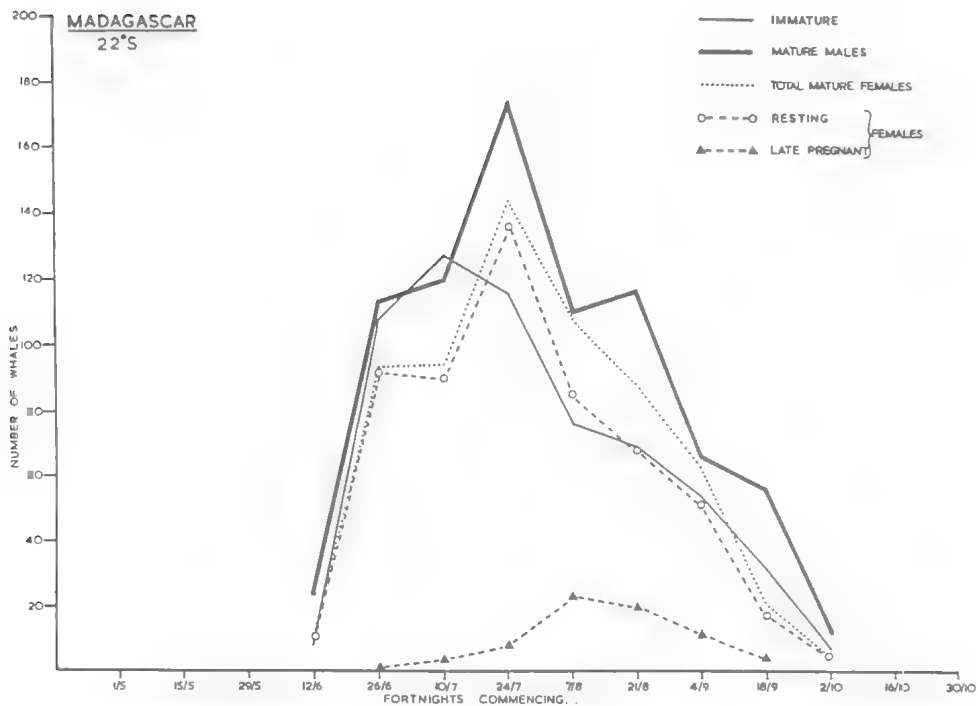


FIG. 19. Fortnightly catches of specified humpback categories, 1948-1949. Madagascar, 22°S.

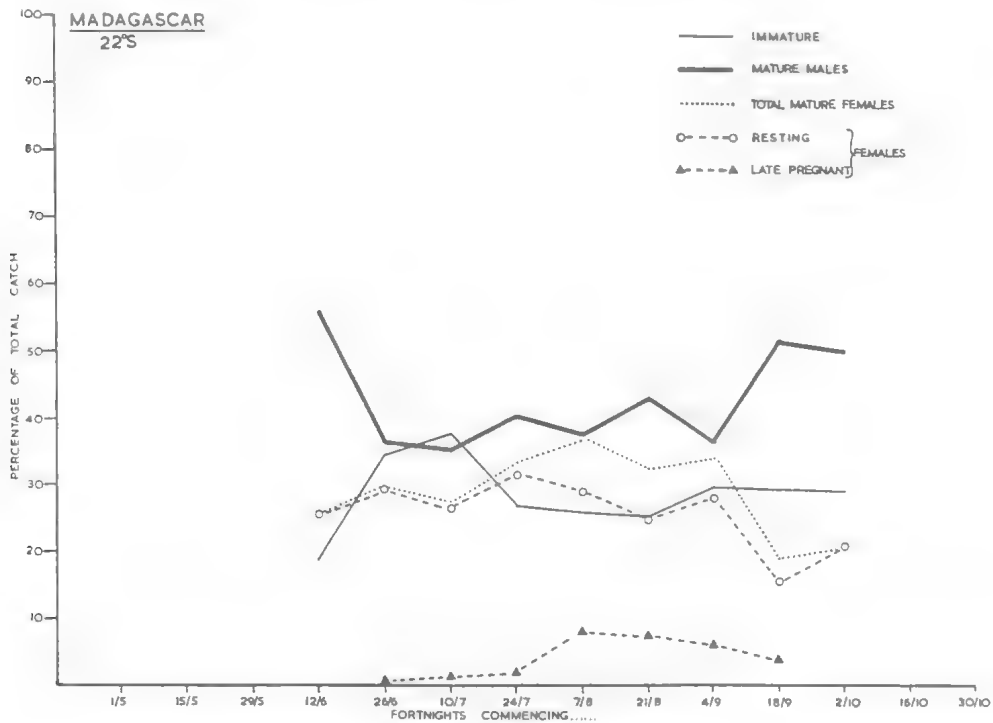


FIG. 20. Fortnightly percentages of specified humpback categories, 1948-1949. Madagascar, 22°S.

TABLE 10. Weekly catches of specified humpbacks, 1948-1949. Madagascar, pelagic, 16°S-26°S.

Start of week	Immature		All immatures	Mature				All humpbacks
	♂	♀		♂	Lact. ♀	R + U ♀	Preg. ♀	
12/6	5	1	6	13		9	0	28
19/6	0	2	2	11		2	0	15
26/6	17	14	31	44		28	0	103
3/7	36	40	76	69		64	1	210
10/7	28	35	63	47		53	1	164
17/7	34	30	64	73		37	3	177
24/7	27	33	65	91		68	4	228
31/7	24	27	51	83		68	4	206
7/8	21	32	53	66		54	9	182
14/8	9	14	23	44		31	14	112
21/8	13	21	34	45		38	15	132
28/8	12	23	35	72		30	5	142
4/9	13	13	26	47		39	8	120
11/9	17	11	28	19		12	3	62
18/9	9	10	19	20		12	2	53
25/9	6	7	13	36		5	2	56
2/10	0	6	6	11		3	0	20
9/10	1	0	1	1		2	0	4
Total	272	324	596	792		555	71	2014

caught during operations for cows and calves have a calculated mean date of August 29, which is 16 days earlier than for cows and calves. If allowance is to be made for immature whales that precede cows and calves, then the above difference in time would have to be increased. Table 13 shows that (except for one animal) cows and calves have been caught for approximately one month longer than immature humpbacks.

**ANTARCTIC WATERS.** It has been shown elsewhere (Dawbin, 1966) that the composition of the post-war catch samples show no significant difference between those caught in late December and those in early February. Pre-war samples in the 1932-1933 to 1938-1939 seasons included 13,357 catches between early November and late March. These were distributed between the south Atlantic Ocean and the eastern portion of the South Indian Ocean. This area includes regions with substantial differences in sea temperatures at equivalent latitudes and dates.

On the hypothesis that humpbacks would enter Antarctic sectors with warmest water earlier than sectors with colder water, a separation of the data

TABLE 11. Weekly catches of specified humpbacks, 1949-1952. Congo, 1°S.

Start of week	Immature		All immatures	Mature				All humpbacks
	♂	♀		♂	Lact. ♀	R + U ♀	Preg. ♀	
5/6	0	1	1	0		1	0	2
12/6	9	13	22	21		19	1	63
19/6	16	21	37	39		34	1	111
26/6	39	48	87	73		46	0	206
3/7	42	37	79	117		81	0	277
10/7	45	54	99	139		77	0	315
17/7	54	56	110	153		85	2	350
24/7	55	50	105	157		101	3	366
31/7	52	54	106	167		93	3	369
7/8	37	47	84	143		103	3	333
14/8	32	42	74	123		77	4	273
21/8	29	37	66	136		93	10	310
28/8	18	17	35	121		79	7	242
4/9	18	16	34	121		81	4	240
11/9	10	10	20	105		65	1	191
18/9	3	10	13	103		56	4	176
25/9	6	4	10	53		46	1	110
2/10	2	3	5	51		27	0	83
9/10	2	1	3	23		14	1	41
16/10	0	1	1	2		5	0	8
Total	469	522	991	1847		1188	45	4071

into sectors of 20° longitude was made. Only two of these (20°E to 39°E and 80°E to 99°E) contained samples adequate for analysis. However, in the former sector cold water extends further north than in the latter at the same dates. Table 19 shows that by using mean dates as an index, humpbacks occur about three weeks later than in the latter sector.

Within each sector one would expect changes in local catch composition during the period that each category of humpbacks arrives or departs from Antarctic waters. In view of the consistently slow rate of humpback migration through a wide range of latitudes (Dawbin, 1966) and the relatively consistent difference in time sequence between categories in temperate and tropical waters as described previously, it seemed probable that time sequence changes would occur first at more northerly latitudes, e.g., 55°S and would be more or less duplicated at a later date in higher latitudes, e.g., 60°S or 66°S. To test this hypothesis the catch samples within sectors were subdivided into three degree lines of latitude. In the absence

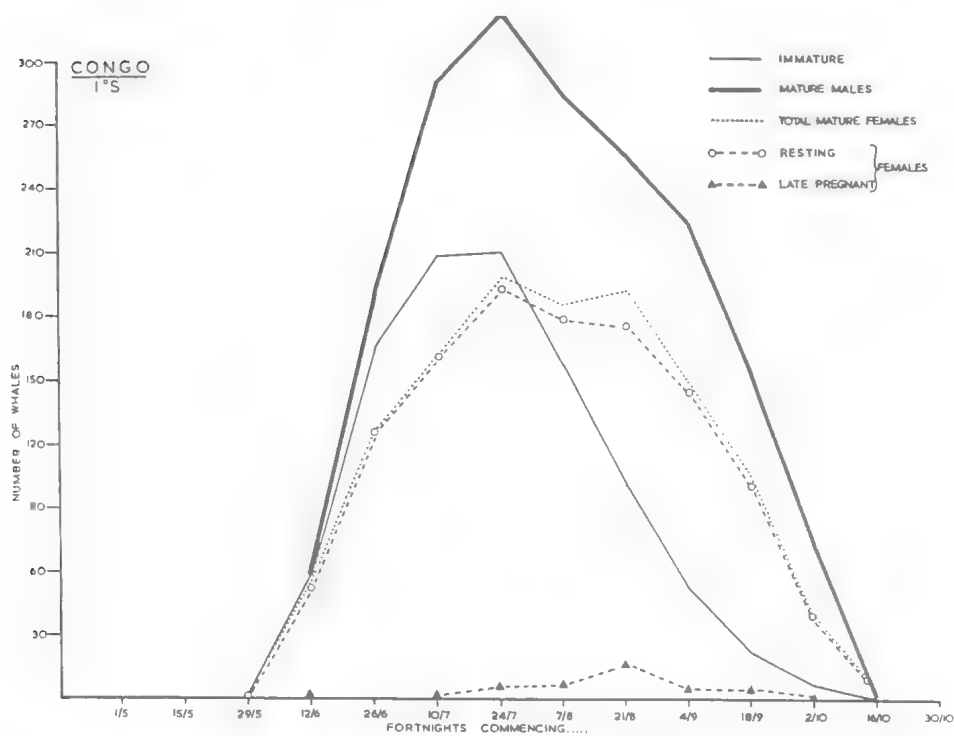


FIG. 21. Fortnightly catches of specified humpback categories, 1949-1952. Congo, 1°S.

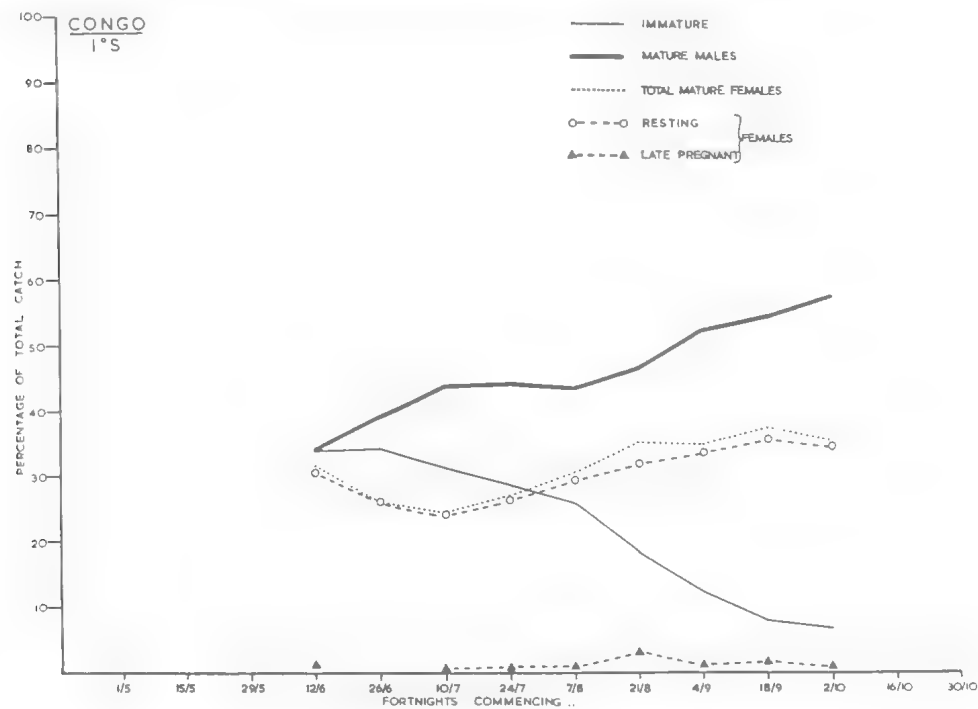


FIG. 22. Fortnightly percentages of specified humpback categories, 1949-1952. Congo, 1°S.

TABLE 12. Estimated mean date with standard deviation and the 95% confidence limits of the mean for specified categories of northbound humpbacks. \* Since mixed females form a heterogeneous group, these data are not strictly comparable with those relating to the more homogeneous categories.

	Mean date	Week code mean	SD (n)	Confidence limits
Cook Strait, NZ, 41°S				
Lact. ♀	June 6	5.84	1.81 (120)	0.33
Immature	June 14	6.94	2.32 (620)	0.19
Mature ♂	June 29	9.00	2.53 (802)	0.18
Resting ♀	July 1	9.32	2.74 (216)	0.37
Preg. ♀	July 8	10.34	2.21 (164)	0.35
All	June 24	8.29	2.76 (1922)	0.13
Great Barrier Is., NZ, 36°S				
Immature	June 19	7.63	1.70 (73)	0.40
Mixed ♀ R+U	June 25	8.56 *	2.42 (41) *	0.76 *
Mature ♂	June 30	9.27	2.27 (106)	0.44
Preg. ♀	July 8	10.36	1.41 (11)	0.86
All	June 26	8.68	2.24 (231)	0.29
Albany, WA, 35°S				
Lact. ♀	June 28	8.93	2.26 (69)	0.54
Immature	July 6	9.98	2.51 (164)	0.25
Mature ♂	July 16	11.50	2.42 (389)	0.28
Resting ♀	July 20	12.10	2.34 (112)	0.44
Preg. ♀	July 30	13.52	1.87 (65)	0.46
All	July 14	11.17	2.64 (699)	0.20
Durbart, Natal, 30°S				
Immature	July 7	10.23	2.52 (332)	0.27
Mature ♂	July 9	10.46	2.11 (212)	0.29
Mixed ♀ R+U	July 12	10.88 *	2.50 (123) *	0.47 *
All	July 8	10.42	2.40 (667)	0.19
Byron Bay, E Australia, 29°S				
Immature	July 4	9.90	3.10 (39)	1.00
Mature ♂	July 8	10.35	2.51 (414)	0.25
Mixed ♀ R+U	July 15	11.35 *	2.64 (204) *	0.37 *
Preg. ♀	July 22	12.28	1.80 (32)	0.64
All	July 10	10.75	2.63 (689)	0.20
Norfolk Is., 29°S				
Mature ♂	July 23	12.44	2.86 (282)	0.34
Immature	July 25	12.73	2.76 (60)	0.72
Mixed ♀ R+U	Aug. 2	13.98 *	3.30 (99) *	0.66 *
All	July 25	12.63	3.01 (441)	0.28

	Mean date	Week code mean	SD (n)	Confidence limits
Moreton Is., E Australia 27°S				
Mature ♂	July 9	10.48	2.62 (3347)	0.09
Immature	July 11	10.72	2.96 (571)	0.25
Mixed ♀ R+U	July 15	11.30 *	2.91 (1164) *	0.17 *
Preg. ♀	July 25	12.76	1.78 (135)	0.31
All	July 11	10.75	2.75 (5217)	0.08
Carnarvon, WA, 25°S				
Lact. ♀	June 28	8.97	2.09 (523)	0.18
Immature	July 18	11.83	3.10 (636)	0.25
Resting ♀	July 26	12.90	2.60 (1087)	0.15
Mature ♂	July 28	13.20	2.81 (2209)	0.12
Preg. ♀	Aug 3	14.03	2.98 (68)	0.72
All	July 23	12.46	3.05 (4523)	0.09
Point Cloates, WA, 22.5°S				
Lact. ♀	July 9	10.50	2.10 (176)	0.31
Immature	July 20	12.08	2.30 (416)	0.22
Mature ♂	July 28	13.22	2.02 (870)	0.13
Resting ♀	July 28	13.23	1.98 (375)	0.20
Preg. ♀	Aug 1	13.80	2.83 (159)	0.38
All	July 25	12.79	2.32 (1996)	0.10
Madagascar, 16°S-29°S				
Immature	July 28	13.20	2.95 (529)	0.25
Mixed ♀ R+U	July 30	13.56	3.04 (521)	0.27
Mature ♂	July 31	13.69	3.14 (705)	0.24
Preg. ♀	Aug 16	15.95	2.10 (64)	0.52
All	July 31	13.59	3.06 (1819)	0.14
Congo, 1°S				
Immature	July 29	13.35	3.43 (991)	0.22
Mature ♂	Aug 11	15.23	4.10 (1847)	0.19
Mixed ♀ R+U	Aug 11	15.23	4.19 (1188)	0.24
Preg. ♀	Aug 21	16.69	3.26 (45)	0.99
All	Aug 8	14.79	4.07 (4071)	0.18

of recognisable trends within this grouping, the data were pooled into two main groups of six degree lines including 55°S-60°S and 61°S-66°S (both inclusive) within each sector.

A few humpbacks only were caught within these sectors and latitudes during the 1932-1933 and 1933-1934 seasons, so these were eliminated in an attempt to reduce error due to seasonal variation. After these steps, the remaining samples between 55°S and 66°S included 5030 humpbacks in the sectors between 20°S to 39°S

and 3938 in the sector between 80°E and 99°E. The weekly catch results are shown in Tables 15-18, and the fortnightly numbers and percentage groupings in Figs 26-27.

The results appear to be so inconsistent, whether considered by the above sectors and latitude groupings, or a variety of subdivisions within these, that the writer is unable to suggest any general trend in the order of arrival and departure of different humpback categories. It is clear that in Antarctic waters humpbacks, in general, are caught earlier in the sector of warmer waters (80°E to 99°E) than in the colder water sector and earlier in low latitudes (55°S to 60°S) than in higher latitudes (see also Table 19). However,

Table 13. Weekly catches of specified humpbacks, 1957-1961. Tonga, 22°S.

Start of week	Immature		All immatures	Mature				All humpbacks
	♂	♀		♂	Lact. ♀	R + U ♀	Preg. ♀	
24/7			1					1
31/7			1		2			3
7/8			2		1			3
14/8			5		2			7
21/8			3		7			10
28/8			3		8			11
4/9			4		2			6
11/9			2		9			11
18/9			1		12			13
25/9			1		2			3
2/10			2		3			5
9/10					4			4
16/10					1			1
23/10			1		2			3
30/10								
6/11					1			1
Total			26		56			82

even this finding may be more a description of the movement of factory ships in relation to the edge of the pack ice than a true indication of humpback movements.

If differences in actual mean dates for all humpbacks at each of the four regions are disregarded for the purposes of discussion, it is still clear from Figs 26-27 and Table 19, that there are very small and inconsistent differences in the relative timing of humpback categories within each region.

Based on mean dates, there is a maximum difference of nine days between the earliest and last of the four identifiable humpback categories. Even within this limited period, the apparent sequence on mean dates is different within each of the four groupings (Table 19). The catch composition also differs substantially in fortnightly frequency (Figs 26-27). If the catch is an adequate sample of the local humpback composition, then the above results indicate that movements of different humpback categories in Antarctic waters between late November and mid-March are mainly random.

There are several factors that may contribute to this negative result. In Antarctic waters, the movements of factory ships and chasers have been directed primarily towards catching fin and

TABLE 14. Estimated mean date with standard deviation and the 95% confidence limits of the mean for specified categories of southbound humpbacks.

	Mean date	Week code mean	SD (n)	Confidence limits
Tonga, 22°S				
Immature	Aug 29	17.78	3.36 (28)	1.27
Lact. ♀	Sept 14	20.04	3.01 (56)	0.80
All	Sept 9	19.29	3.29 (84)	0.72
Moreton Is., E Australia, 27°S				
Mixed ♀ R+U	Sept 6	18.96	1.83 (183)	0.27
Immature	Sept 8	19.21	1.95 (249)	0.25
Mature ♂	Sept 13	19.96	2.22 (545)	0.18
All	Sept 11	19.58	2.13 (977)	0.13
Byron Bay, E Australia, 29°S				
Mixed ♀ R+U	Sept 4	18.69	1.70 (100)	0.58
Immature	Sept 14	20.11	2.20 (57)	0.45
Mature ♂	Sept 22	21.22	2.47 (191)	0.35
All	Sept 16	20.31	2.48 (348)	0.27
Norfolk Is., 29°S				
Mixed ♀ R+U	Sept 24	21.44	1.86 (160)	0.30
Immature	Sept 24	21.52	1.86 (66)	0.46
Mature ♂	Oct 8	23.52	1.86 (213)	0.25
All	Oct 1	22.46	2.12 (439)	0.20
Great Barrier Is., NZ, 36°S				
Immature	Oct 7	23.39	2.36 (13)	1.41
Mixed ♀ R+U	Oct 8	23.47	2.17 (15)	1.18
Mature ♂	Oct 24	25.80	0.50 (5)	0.59
All	Oct 17	23.79	2.22 (33)	0.77

blue whales with humpbacks as a rather secondary objective. In coastal areas such as the offshore waters from Durban, it has already been argued that such selection might significantly affect catch composition. However, there is no substantial evidence to show that such differential selection will invalidate humpback sampling on the open seas distant from shore lines.

As a more simple hypothesis, I suggest that the catch sample has been taken after a large proportion of the humpbacks had already reached Antarctic waters, and that sampling ended before any significant emigration from the region had commenced.

The season during which southbound humpbacks pass many tropical and temperate localities is known, and at an overall migration rate of 15° per month (Dawbin, 1966), it can be shown that in most sectors more than half of all humpbacks could be expected south of 55°S by late November. If the sequence followed in warmer waters is still maintained during progress into high latitudes, then all main categories of humpbacks



should already be represented south of 55°S before December, with the possible exception of cows accompanied by calves. Cows accompanied by calves receive full protection, and therefore do not contribute to the catch. The absence of samples during much of the period of entry into high latitudes would contribute greatly to a masking of trends.

The period of emigration from Antarctic waters as calculated from the time of appearance of northbound humpbacks at lower latitudes, indicates that very few animals are likely to pass north of 55°S until late April, i.e., after catch sampling in high latitudes has ceased. Similar calculations for 60°S and other high latitudes are consistent with the view that the catch sampling in Antarctic waters during 1934-1939 occurred during months in which entry and exit of humpbacks was too small to become evident.

Catches were made during considerably longer seasons in the Falkland Island Dependencies region 1910 to 1917. Data from these catches have been examined, but they include such wide differences between individual companies operating in proximity to each other that the writer has failed to establish consistent trends.

It should be noted that these early records were made at a time when many whales were dismembered alongside anchored factory ships, thus adding difficulties in obtaining accurate length measurements, and complicating any examination for foetuses. Inspectors concerned primarily with catch examination were not required by International regulations until 1937.

### CONCLUSIONS

Northbound humpbacks have been sampled by catches between 41°S and 1°S and include mate-

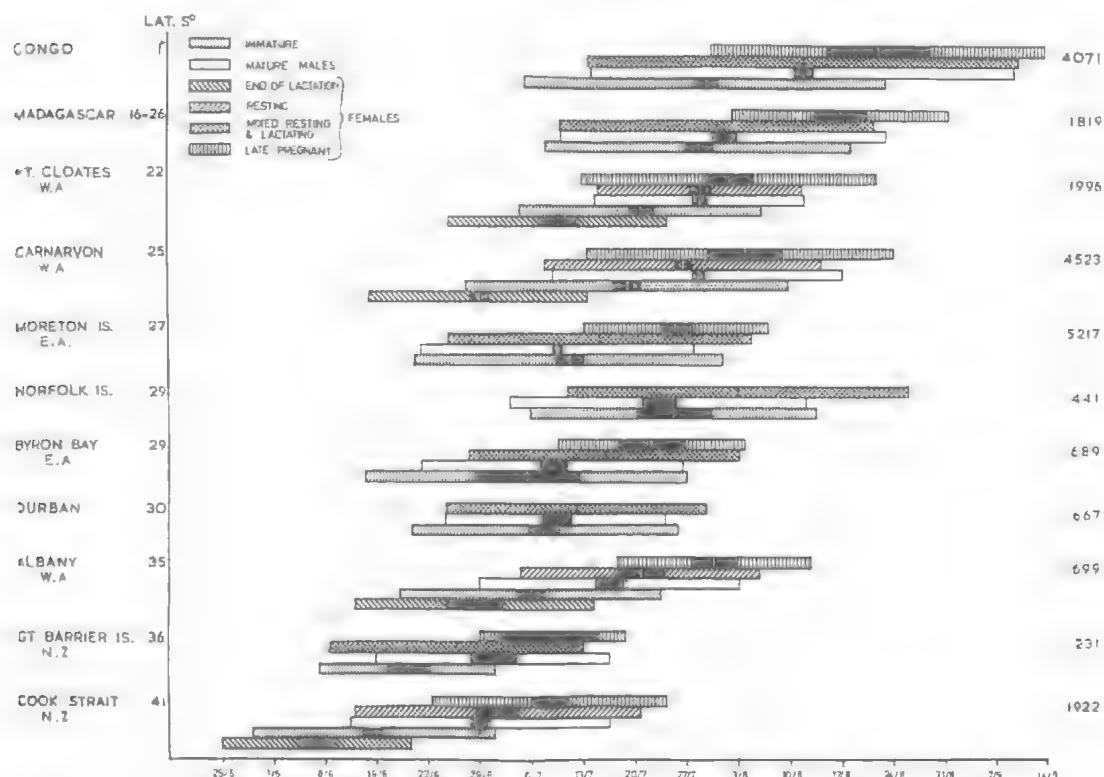


FIG. 23. The period of passage of specified northbound humpbacks as shown by catch composition in temperate and tropical waters. Mean date for each category shown as vertical white line. 95% confidence limits for the mean shown in black. One standard deviation either side of the mean shaded.

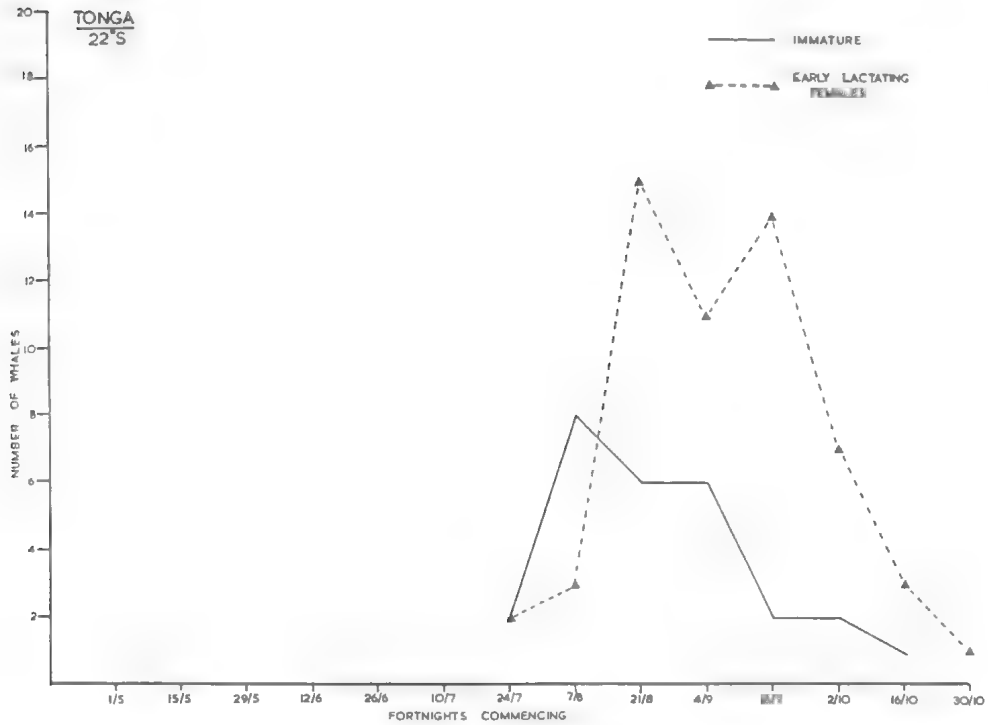


FIG. 24. Fortnightly catches of southbound immature humpbacks and lactating females, 1957-1961. Tonga, 22°S.

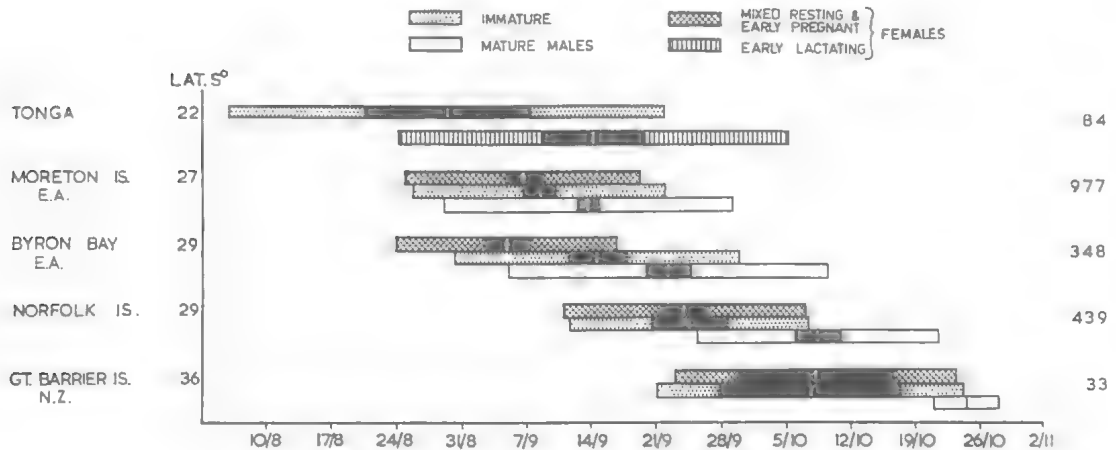


FIG. 25. The period of passage of specified southbound humpbacks as shown by catch composition in temperate and tropical waters. Mean date for each category shown as vertical white line. 95% confidence limits for the mean shown in black. One standard deviation either side of the mean shaded.

TABLE 15. Weekly catches of specified humpbacks, 1934/35 to 1937/38. Longitudes 20°E-39°E, latitudes 55°S-60°S.

Start of week	Immature		All immatures	Mature			All humpbacks
	♂	♀		♂	R + U ♀	Preg. ♀	
6/11						1	1
13/11	3	5	8	1	2	1	12
20/11		1	1				1
27/11	6	7	13	24	24	2	63
4/12	15	17	32	88	112	11	243
11/12	63	104	167	186	186	33	572
18/12	86	77	163	164	121	20	468
25/12	49	51	100	182	118	29	429
1/1	53	56	109	156	96	30	391
8/1	47	66	113	156	102	19	390
15/1	34	30	64	106	73	21	264
22/1	15	16	31	46	49	20	146
29/1	30	29	59	207	101	57	424
5/2	5	13	18	42	20	16	96
12/2	1		1	3	4	2	10
19/2	9	11	20	11	9	8	48
26/2	11	17	28	20	17	4	69
5/3	13	14	27	10	15	1	53
12/3				1		1	2
Total	440	514	954	1403	1049	276	3682

rial relating to at least four segregated breeding stocks. These stocks include one or more groups that pass between east Australia and Tonga, one along west Australia, another past Madagascar and another along West Africa to the Congo. Despite the sampling differences between localities as described in the text, catches from all these stocks share similarities in the time sequence followed by specified categories of humpbacks (Fig. 23, Table 12).

Females at the end of lactation and still accompanied by weaning 'yearlings' occur earliest at all localities from which the data allow identification of this group. At Cook Strait, Albany, Carnarvon and Point Cloates, they occur at an average of 12 days earlier than immature whales. There is no regular difference in timing between immature males and immature females. Mature males follow immature whales at Cook Strait, Great Barrier Island, Albany, Durban, Carnarvon, Point Cloates, Madagascar and Congo by an average of 8 days later. As described previously, there is no significant difference in timing between these categories at the three stations where quotas and

TABLE 16. Weekly catches of specified humpbacks, 1934/35 to 1937/38. Longitudes 20°E-39°E, latitudes 61°S-66°S.

Start of week	Immature		All immatures	Mature			All humpbacks
	♂	♀		♂	R + U ♀	Preg. ♀	
4/12		1	1	3			4
11/12		1	1				1
18/12	1		1				1
25/12	1	1	2	1	9	1	13
1/1	1	9	10	6	11	3	30
8/1	2	3	5	7	9	4	25
15/1	1	2	3	9	12	7	31
22/1	6	5	11	25	37	12	85
29/1	9	10	19	26	19	15	79
5/2	29	37	66	119	93	30	308
12/2	20	32	52	60	65	26	203
19/2	40	41	81	124	66	28	299
26/2	5	6	11	28	8	6	53
5/3	10	8	18	28	15	5	66
12/3	5	2	7	13	12	2	34
19/3	5	4	9	4	1		14
26/3				62	19	12	102
Total	135	162	297	515	376	151	1348

intense selection for large animals has resulted in marked under-representation of immature animals (Byron Bay, Norfolk Island, Moreton Is-

TABLE 17. Weekly catches of specified humpbacks, 1934/35 to 1937/38. Longitudes 80°E-99°E, latitudes 55°S-60°S.

Start of week	Immature		All immatures	Mature			All humpbacks
	♂	♀		♂	R + U ♀	Preg. ♀	
16/11	2	3	5	3	10	16	34
13/11				1	6	18	25
20/11	8	7	15	16	49	28	108
27/11	5	23	28	21	84	13	146
4/12	26	31	57	104	138	50	344
11/12	19	32	51	100	85	49	285
18/12	21	32	53	132	146	56	387
25/12	4	12	16	55	64	51	186
1/1	4	9	13	30	45	33	121
8/1	4	18	22	43	45	9	119
Total	93	167	260	505	667	323	1755

TABLE 18. Weekly catches of specified humpbacks, 1934/35 to 1937/38. Longitudes 80°E-99°E, latitudes 61°S-66°S.

Start of week	Immature		All immatures	Mature			All humpbacks
	♂	♀		♂	R + U ♀	Preg. ♀	
27/11						1	1
4/12		3	3	2	1	1	7
11/12	3	6	9	1	2	9	21
18/12	12	20	32	36	17	23	108
25/12	16	17	33	59	53	23	168
1/1	12	11	23	38	18	35	114
8/1	17	25	42	55	65	42	204
15/1	28	33	61	64	53	39	217
22/1	41	57	98	100	72	42	312
29/1	20	35	55	78	65	33	231
5/2	28	29	57	100	61	23	241
12/2	28	25	53	84	95	14	246
19/2	34	40	74	62	54	12	202
26/2	13	11	24	21	21	9	75
5/3	1	4	5	13	9	8	35
Total	253	316	569	713	587	314	2183

land). However, there is no case in which mature males have preceded immature whales by an amount that is significant at the 5% level.

Mature females that are predominantly in the resting condition have occurred at an average of only 3 days after mature males so can be regarded as following a similar time sequence to the latter. The apparent timing of mixed females is variable due to the unknown but certainly different proportions of late lactating and resting animals included in this group at different localities. For this reason it is not strictly comparable with the more accurately specified categories. In general, mixed females have a mean date which falls after those for immature whales and before those for pregnant females. Pregnant females have been represented at all localities except Norfolk Island and Durban. In all cases where they are represented, they occur as the last northbound category. The average intervals are 11 days after mature males, 19 days after immature animals and 31 days after lactating females.

Due to sampling errors discussed previously, the above time intervals are not regarded as having the precision implied by expressing the results in days, but the results should be a reasonable indication of the order of time difference between categories. For the reasons given previously, it is

TABLE 19. Estimated mean date with standard deviation and the 95% confidence limits of the mean for specified categories of Antarctic humpbacks.

	Mean date	Week code mean	SD (n)	Confidence limits
80°-99°E, 55°-60°S				
Preg. ♀	Dec 13	5.94	2.33 (323)	0.26
Non-preg. ♀	Dec 14	6.10	2.04 (667)	0.16
Immature	Dec 14	6.11	1.98 (260)	0.25
Mature ♂	Dec 18	6.58	1.76 (505)	
All	Dec 15	6.21	2.02 (1755)	0.10
80°-99°E, 61°-66°S				
Preg. ♀	Jan 19	11.23	2.92 (314)	0.33
Mature ♂	Jan 27	12.33	2.84 (713)	0.21
Immature	Jan 27	12.34	2.94 (569)	0.25
Non-preg. ♀	Jan 28	12.51	2.81 (589)	0.23
All	Jan 26	12.22	2.90 (2185)	0.12
20°-39°E, 55°-60°S				
Non-preg. ♀	Jan 2	8.77	3.17 (1049)	0.20
Immature	Jan 4	9.10	3.33 (954)	0.22
Mature ♂	Jan 5	9.25	3.01 (1403)	0.16
Preg. ♀	Jan 11	10.13	3.24 (276)	0.39
All	Jan 4	9.14	3.18 (3682)	0.10
20°-39°E, 61°-66°S				
Non-preg. ♀	Feb 11	14.55	2.74 (376)	0.28
Preg. ♀	Feb 13	14.77	2.73 (151)	0.45
Immature	Feb 14	14.88	2.49 (297)	0.29
Mature ♂	Feb 19	15.62	2.85 (515)	0.25
All	Feb 15	15.06	2.76 (1339)	0.15

probable that the differences described here are minimal and likely to be greater in the migrating population than shown by catch samples.

Southbound humpbacks form a smaller and more complex sample which has been discussed at greater length elsewhere (Dawbin, 1966). Based on mean dates, mixed females together with immature animals, form the earliest southbound categories (Fig. 25, Table 14). In these cases, mixed females include those in very early pregnancy unseparated from resting females. Many of these females would correspond to those that travelled north early when at the end of lactation. If these females also returned south early, then many would be incorrectly included amongst the northbound whales which overlap with southbound up to the time that 50% are sighted travelling north and 50% travelling south. This, combined with a lack of data on which to separate early pregnant from resting females impedes attempts to estimate a mean time interval for these females (see also Dawbin, 1966), but they clearly precede mature males and cows with

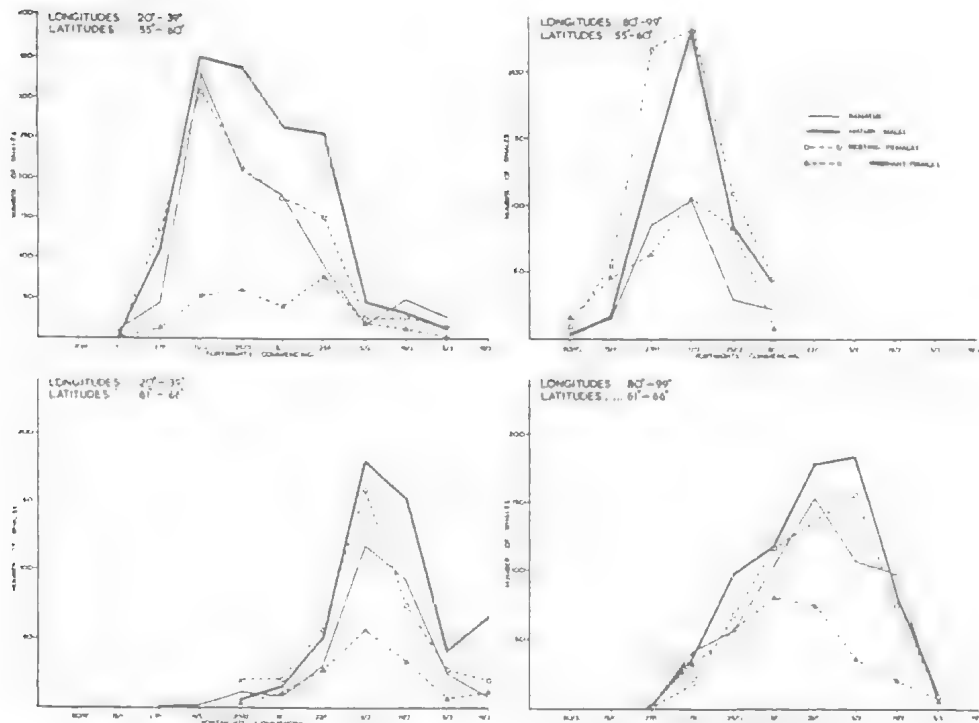


FIG. 26. Fortnightly catches of specified humpback categories, Antarctic, 1934/35 to 1938/39 seasons. Longitudes 20°E to 39°E and 80°E to 99°E, latitudes 55°S to 60°S and 61°S to 66°S for each longitude group.

calves and the data are not inconsistent with the view that many may precede immature humpbacks.

Immature humpbacks travel south about 10 days earlier than mature males and the latter in turn precede cows accompanied by young calves. Subtraction of the 10 days' difference between immature animals and mature males as above, from the 16 days' difference between immature animals and cows with calves at Tonga appears to indicate a difference of 6 days only (figure used by Dawbin, 1966) between mature males and cows with calves. However, reasons for believing that the calculated interval at Tonga is an underestimate have been discussed previously. In addition, the observations of Chittleborough near Point Cloates 22°S (1953) and Bryon Bay 28°S (1962) together with those of the writer in Foveaux Strait 48°S, have shown that cows accompanied by calves comprise considerably more than 50% of all humpbacks at these latitudes during the final three or four weeks of the southward migration past each locality. Thus any non-

lactating females and late immature animals together with mature males, are considerably outnumbered by cows and calves at this stage. The latter, which comprise the females that travelled north last as pregnant animals, are clearly the last category to return south. The available data on the time sequence of southbound humpbacks is not inconsistent with the view that humpbacks return south in approximately the same sequence as they follow during the migration north.

Antarctic catch samples, when subdivided according to latitudes and sectors of longitude, indicate differing time sequences between samples. There is, therefore, no consistent trend recognisable in the present analysis of Antarctic catches. Since most of the samples were obtained after late November, it seems probable that they were obtained from a population that had already stabilised considerably as a result of the arrival of most catchable categories into the Antarctic sampling zone. This hypothesis is consistent with the expected arrival dates based on known mean dates in lower latitudes and a migration rate of

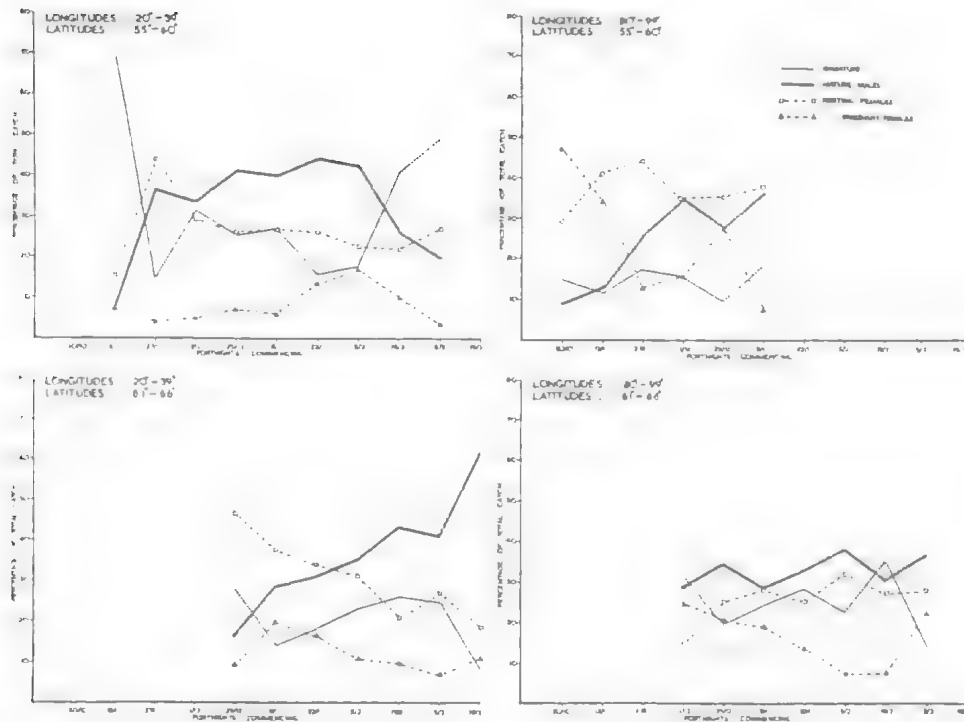


FIG. 27. Fortnightly percentages of specified humpback categories, antarctic, 1934/35 to 1938/39 seasons. Longitudes 20°E to 39°E and 80°E to 99°E, latitudes 55°S to 60°S and 61°S to 66°S for each longitude group.

about 15° per month. On the same evidence, no consistent changes in composition would be expected before the northward departure of some humpbacks in mid to late April, i.e., considerably later than the period during which catch sampling occurred. In the absence of consistent trends in Antarctic samples, the order in which the specified humpback categories travel past each locality and the time intervals between the earliest and each of the later categories have been estimated exclusively from temperate and tropical data.

The estimated humpback sequences differ markedly from those of fin whales described by Laws (1961) who discusses extensive Antarctic data and the findings of previous workers, especially Mackintosh (1942). Laws concludes that both the north and south migrations of older fin whales and of pregnant females are in advance of those of other groups, and that sexually immature animals are later. Pregnant humpbacks appear to travel south in advance of other humpbacks, but return north after other categories. Immature

humpbacks are the second group in both south and north migrations, followed by mature males together with resting females, while lactating females travel south last and return north in advance of other humpbacks.

There is no consistent evidence that different humpback categories either migrate at different speeds or stay for significantly different lengths of time in the breeding areas. The data indicate that most categories depart also from the feeding areas in the same order as they arrive. Most categories therefore spend more or less equal periods in Antarctic waters. The main exception are breeding females which, when pregnant, spend a prolonged period in the feeding regions and, when lactating, spend an abridged period, while resting females stay for approximately the same length of time as mature males and immature humpbacks.

The implications of these findings in relation to the breeding cycle and the environmental conditions encountered during migration are discussed more fully elsewhere (Dawbin, 1966).

## ACKNOWLEDGEMENTS

Mr E. Vangstein with the permission of the managers of southern hemisphere whaling companies has provided a major part of the post-war daily catch data. Dr R.G. Chittleborough has supplied much supplementary data on Australian catches. Professor J.T. Rudd supplied catch data on pre-war temperate and tropical catches, and Dr F.C. Fraser on catches in the Falkland Island Dependencies area. Dr N.A. Mackintosh has encouraged and discussed the study throughout. Mr G.T. & J.H. Perano and staff at the Cook Strait Whaling Station have assisted greatly in the collection of much material as well as catch data from New Zealand catches. I have greatly appreciated this assistance, and I wish to thank all those who have helped in this study.

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TWO NEW GENERA OF ACANTHODRILINAE (MEGASCOLECIDAE,  
OLIGOCHAETA) FROM CAPE YORK PENINSULA AND THE TORRES STRAIT

G.R. DYNE

Dyne, G.R. 1997 06 30: Two new genera of Acanthodrilinae (Megascolecidae, Oligochaeta) from Cape York Peninsula and the Torres Strait. *Memoirs of the Queensland Museum* 42(1): 139-157. Brisbane. ISSN 0079-8835.

Two new meronephric genera of Australian acanthodrilid earthworms from Cape York Peninsula and the Torres Strait are described: *Neodiploptrema* gen. nov., with seven new species, and *Torresiella* gen. nov., with a single new species. All are considered to be local derivatives of the holonephric endemic Australian genus *Diploptrema*. Six species of *Neodiploptrema* show the acanthodrilin condition of the male genital terminalia, with male pores on segment XVIII and a pair of prostatic pores on each of segments XVII and XIX, but one species exhibits the microscolecin reduction in which male pores have been translocated forwards to unite with a single pair of prostatic pores, in XVII. Two species of *Neodiploptrema* have modifications of the nephridial system which pose difficulties for the existing classification of the Megascolecidae. *Torresiella* shows the rare balantini reduction in which the male pores have been translocated posteriorly to unite with a single pair of prostatic pores, in XIX. □ Acanthodrilinae, Megascolecidae, *Neodiploptrema*, *Torresiella*, oligochaetae.

G.R. Dyne, Environment Australia, GPO Box 787 Canberra ACT 2600, Australia; 24 April 1997.

Prior to the present work, the Australian genera of earthworms of the subfamily Acanthodrilinae have been exclusively holonephric, with a pair of stomate nephridia in each typical body segment. In contrast, Lee (1959, 1970) clearly demonstrated close affinity between holonephric New Zealand acanthodrilid genera and those with more than one pair of nephridia per segment, the meronephric condition, and concluded that local transition from holonephry to meronephry had occurred. Two meronephric genera of Australian acanthodrilids are here described which are considered to be similarly localised derivatives of the endemic holonephric genus *Diploptrema*.

*Diploptrema* has been demonstrated to have an extensive range, from the vicinity of Narrabri, New South Wales, to northern Queensland and across northern Australia to the Kimberley region of Western Australia. (Mackenzie & Dyne, 1991; Jamieson & Dyne, 1976; Dyne, 1979). The precise northerly limit of the genus in Cape York Peninsula is unknown, the most northerly definitive record coming from the vicinity of Weipa (Dyne, 1984). It is thus uncertain whether *Neodiploptrema* effectively replaces *Diploptrema* from a certain point northwards. However, the two genera are sympatric in the Cape Melville National Park and McIlwraith Range (Jamieson, 1997, this volume).

Despite recent efforts to improve knowledge of the biota of the region generally (e.g., Glasco et al., 1995), the earthworm fauna of Cape York

Peninsula and the Torres Strait remains poorly understood. Apart from species of the pheretimoid genus *Begemius* described by Easton (1982), this paper constitutes the only account of endemic earthworm taxa from the region.

Abbreviations used. ANIC = Australian National Insect Collection, coll. = collected by, gm = genital marking, GD = Author's collection, H = holotype, P = paratype, pr. p = prostatic porophore, p.s.p. = penial seta pore, QM = Queensland Museum, Sp. p = spermathecal pore. Scale-bars = 1mm in all figures.

*Neodiploptrema* gen. nov.

**DIAGNOSIS.** Setae 8 per segment. Prostates 2 pairs, tubular, their pores on XVII and XIX, or, exceptionally, a single pair, on XVII. Male pores present in XVIII, or, rarely (microscolecin condition), closely associated with a single pair of prostatic pores on XVII. Spermathecal pores 2 pairs, in 7/8 and 8/9, or a single pair, in 8/9 only. Gizzard very well-developed, in V. Calciferous glands present or absent. Meronephric, avesculate; anterior tufted nephridia present. Holandric, or, exceptionally, metandric. Testis-sacs absent. Penial setae invariably present; genital setae usually present, but occasionally lacking.

**DESCRIPTION.** Small to large terrestrial worms (48-465mm in length) with 130-500 segments. Body circular in cross-section. Prostomium pro-



FIG. 1. Map showing recorded occurrences of *Neodiploptrema* and *Torresiella*.

epilobous to epilobous. Dorsal and median ventral groove absent. Dorsal pores commencing from 8/9 to 11/12. Setae closely paired, commencing on II; ventral intersetal distance (*aa*) not greatly different from that (*bc*) separating the lateral setae; ventral and dorsal setal couples of similar width; dorsal median intersetal distance (*dd*) > 45% of the body circumference in the forebody. Setae of XVIII, or the ventral setal couples lacking; ventral setal couples of XVII and XIX modified as enlarged penial setae, or, rarely, only those of XVII thus modified (in *N. deminutionis*); ventral setal couples of IX modified as enlarged genital setae, or undifferentiated. Nephropores numerous and usually inconspicuous. Clitellum saddle-shaped, or annular, occupying XIII to XVI-XVIII. Two pairs of prostatic pores, equatorial on XVII and XIX, coincident with the penial seta orifices, or (*N. deminutionis*) a single pair of combined male and prostatic pores on XVII. Male pores a pair of openings in seminal grooves (the latter well-developed or very faint), presetally, or far anterior, in XVIII (rarely in the microscolecin arrangement). Accessory genital markings present in some of the segments VIII-XXXII, usually intersegmental, rarely absent. Female pores paired, presetal, median to lateral of *ab*, in XIV. Spermathecal pores

2 pairs, in 7/8 and 8/9, in or near *ab*, exceptionally in 8/9 only.

Some pre-clitellar septa thickened. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII, some of the commissurals posterior of and including X latero-oesophageal, dorso-ventral commissural vessels commencing in VI-VII; supra-oesophageal vessel limited to the oesophagus; subneural vessel absent. Gizzard large, often strongly muscular, in V. Calciferous glands absent, or developed as sessile pouches in the posterior oesophageal region. Intestine commencing in XVII-XX, a dorsal typhlosome well developed. Body astomate, exonephric; caudally nephridial bodies enlarged, each with a pre-septal funnel; extensive tufting present in all or some of segments III-V. Enteronephry not developed. Holandric, sperm funnels free in X and XI, or metandric, the funnels in X absent. Seminal vesicles present in IX and XII, or in XI and XII. Prostatic glands tortuous tubes usually restricted to their segment of origin; posterior pair usually conspicuously smaller than the anterior set, or (*N. deminutionis*) totally lacking; prostatic ducts moderately long to long, muscularised. Penial seta follicles usually with copulatory musculature. Ovaries (conjoined oocytic strings) and medium-sized oviductal funnels present in XIII; ovisacs. Spermathecae subequal, or the posterior pair slightly the larger; the single diverticulum is invariably sessile, and provided with numerous intramural sperm chambers.

**DISTRIBUTION.** Cape York Peninsula: apparently restricted to monsoonal semi-deciduous vine-forests in the Lockerbie, Iron Range and Weipa areas; islands of the Torres Strait (Fig. 1).

**TYPE SPECIES.** *Neodiploptrema tumida* (designated).

**ETYMOLOGY.** Differing from *Diploptrema* in a novel feature (meronephry).

**REMARKS.** The morphological similarities of *Neodiploptrema* to the Australian acanthodriline genus *Diploptrema* are so close, including even the possession of anterior genital setae in some species, that origin of the *Neodiploptrema* from the latter seems indisputable.

#### List of species of *NEODIPLOPTREMA*

- 1) *N. deminutionis* sp. nov., 2) *N. exigua* sp. nov., 3) *N. lacisbrontois* sp. nov., 4) *N. occidentalis* sp. nov., 5) *N. raveni* sp. nov., 6) *N. tumida* sp. nov., 7) *N. varionephrica* sp. nov.

# KEY TO SPECIES OF THE GENUS NEODIPLOTREMA

1. Male apparatus acanthodrilin: 2 pairs of prostatic pores in XVII and XIX, male pores separate, on XVIII . . . . . 2  
Male apparatus microcolecin: a single pair of prostatic pores associated with the male pores on XVII . . . . . *N. deminutionis*
2. Nephridia in the mid-body consisting of a prominent megameronephridium, and 3 small micromeronephridial bodies . . . . . 3  
Nephridia in the mid-body uniform in size or medianmost nephridium not greatly enlarged . . . 4
3. Genital setae present, intestine commencing in XVIII . . . . . *N. varionephrica*  
Genital setae absent, intestine commencing in XX . . . . . *N. exigua*
4. Male organs metandric . . . . . *N. occidentalis*  
Male organs holandric (though there may be some reduction in X) . . . . . 5
5. Genital setae well-developed, in IX; prominent genital markings present in the region XVIII-XXI . . . . . *N. tumida*  
Genital setae absent or rudimentary. Genital markings absent from the region XVIII-XXI . . . 6
6. Moderately large worms (150-200mm); ventral setal couples of XVIII lacking, oesophagus with conspicuous outpouchings in XIV-XV . . . . . *N. lacisbrontoi*  
Very large worms (>350mm); ventral setal couples of XVIII present; oesophageal pouching absent . . . . . *N. raveni*

## *Neodiplotrema deminutionis* sp. nov. (Figs 2, 11B)

TYPE LOCALITY. 10°46'S, 142°34'E., on the eastern side of Lake Bronto, Cape York Peninsula, in open eucalypt forest in dark sandy soil. Coll. R. Raven, 4 Feb 1975.

MATERIAL EXAMINED. HOLOTYPE AND 8 PARATYPES: ANIC GD.95.31.1

DESCRIPTION. Length 71+, 140mm. Width 2.9, 2.7mm. Segments 215+, 311 (Holotype, P2). Uniformly circular in cross-section throughout; pigmentless buff in alcohol. Prostomium prolobous, first dorsal pre-9/10. Setae in regular longitudinal rows, closely paired throughout; ventral setal couples of XVIII normal, those of XVII modified as enlarged penial setae; genital setae lacking. Nephropores inconspicuous. Clitellum not developed in any of the specimens available for study. Combined male and prostatic pores in distinct longitudinal slits on raised papillae, in

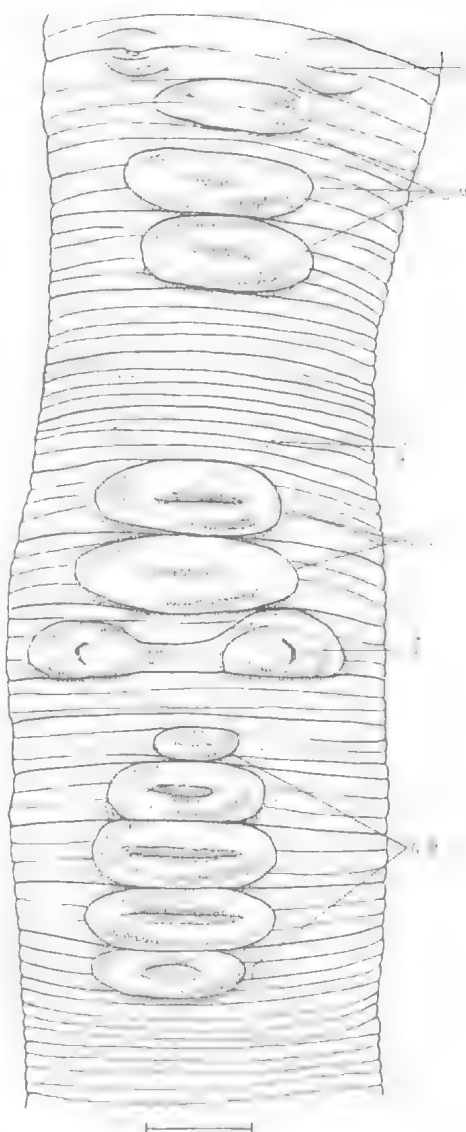


FIG. 2. *Neodiplotrema deminutionis* genital field.

XVII, coincident with the openings of the penial setae. Serial sectioning reveals that the vasa deferentia and prostatic ducts do not actually fuse, but open contiguously at the common pore. Female pores visible as tiny, transverse slits presegmentally, in *ab*, usually with swollen rims. Accessory markings a series of unpaired, median, intrasegmental pads: a small ellipsoidal pad in IX (H, P4-5); a larger one in X, extending across *aa* (H, P1-2, P4-5, P8); a similarly sized swelling in XI (H, P1, P6) (all the above markings have shallow, transversely concave centres); a large

pad is located in XV, transverse width =  $aq$  (H, P1, P3, P5-6), with a larger marking in XVI, across  $bb$  (all specimens excepting P7); another series of similar markings is present in the post-genital region: a diminutive tumescence in XIX (H, P1, P6), a much larger swelling in XX (across  $aa$ ) (H, P1, P6), similarly in XXI (H, P1-6, P8), and a further small marking in XXII (H, P1, P2, P3, P4, P5, P6, P8). In some of the above specimens, the accessory markings are faintly developed.

Septa: 10/11, 11/12 slightly thickened, 6/7-9/10 moderately strongly muscularised, 5/6 slightly thickened, encapsulating the gizzard. Dorsal blood vessel single, continuous onto the pharynx. Supra-oesophageal vessel present VII-XIX, adherent to the roof of the oesophagus, and receiving vessels from oesophageal blood plexi, particularly in XII-XIV. Last hearts in XIII, those in X-XIII receiving thin connectives from the dorsal vessel, and more strongly developed ones from the supra-oesophageal vessels; commissurals XII and XIII much larger than the remainder, which decrease in size anteriorly, those anterior to X dorsoventral only. Gizzard large, shiny, but compressible in V, with a slight dorsoventral compression. Oesophagus rather narrow, constricted intersegmentally, with conspicuous rugae on its inner walls, and extending from VI to XVI. Intestinal origin, commencing with abrupt expansion, in XVII (H), XVI? (P1); somewhat paler and apparently less muscular anterior of XXIV. An extremely well-developed rugose dorsal typhlosole commences in XXII. Metonephric throughout; considerable tufting in IV, with many highly coiled loops, and composite ducts sent to the pharynx; the remainder of the nephridia comprised of very numerous astomate exonephric loops scattered on the body wall and septa, larger and more numerous in the oesophageal region. Caudally, the bodies again enlarged, each apparently with a distinct preseptal nephrostome; no enteronephry demonstrable.

Holandric; 2 pairs of small, iridescent funnels in X and XI, attached ventrally to septa 10/11 and 11/12; large, subequal, racemose seminal vesicles in XI and XII, anteriorly attached to septa 11/12 and 12/13, composed of large, conspicuous loculi. Vasa deferentia obvious as closely paired, slightly iridescent tubes tortuously adherent to the body wall on either side of the oesophagus; the paired ducts become fused in the parietes, in XVII. Prostatic glands a pair of flattened, loosely coiled tubular organs lying in segment XVII, with long, muscular (shiny) ducts opening to the exte-

rior slightly ventral of the vasa deferentia. Penial seta follicles large, gently curving, copulatory musculature well developed, inserted near the mid-dorsal line; the setae with a gradual bend, the shaft divided into an ectal region devoid of ornamentation, with an intervening section bearing scattered solitary or clustered thorn-like spines with rather broad bases, and narrowing to a fine point (these stand out at an angle to the shaft); the entire ectal portion is approximately equal to the ornamented section, and these together constitute about half of the total length of the seta. Length mature seta 2.35mm; midshaft diameter 25.5  $\mu$ m (mean of 3). Ovaries, consisting of thin sheaves of small oocytes, together with medium-sized diaphanous funnels, are present XIII, ovisacs absent. Spermathecae a single pair, divided into a stalked, sacciform ampulla, and a broadly U-shaped diverticulum which is completely sessile, and which occupies the entire dorsal aspect of the short duct: the walls of the diverticulum are studded with numerous iridescent intramural sperm chambers; the ampullal 'stem' is swollen at its junction with the diverticulum. Length right spermatheca of IX 2.6mm (apex of ampulla to pore). Genital seta follicles absent.

**ETYMOLOGY.** Referring to the diminished (microscolecin) condition.

**REMARKS.** As this species is the only known microscolecin *Neodiploptrema*, identification should not prove difficult, particularly when the distinctive array of genital markings is also considered. The latter are atypical of the genus in being intrasegmental. *N. deminutionis* lives in sympatry with *N. lacishrontoi* and *N. vari-onephrica*, but neither of these species appears to be convincing as an acanthodrilin precursor of the former.

***Neodiploptrema exigua* sp. nov.**  
(Figs 3, 11C)

**TYPE LOCALITY** 10°48'S, 142°28'E, Lockerbie East, soil over rocky substrate, in dense semi-deciduous vine-forest. Coll. R. Raven, 1 Feb 1975.

**MATERIAL EXAMINED.** HOLOTYPE, QMGH2889. PARATYPE, QMGH2890. OTHER MATERIAL, 10°48'S, 142°28'E, Lockerbie East, under logs near 'Mango Tree camp', Coll. R. Raven, 30 Jan 1975 (3 immature-semi-mature specimens, not designated as types, ANIC GD.95.9.3).

**DESCRIPTION.** Length 48, 64mm. Width (mid-clitellar) 1.7mm. Segments 149, 136 (Holotype, P1). Uniformly circular in cross-section,

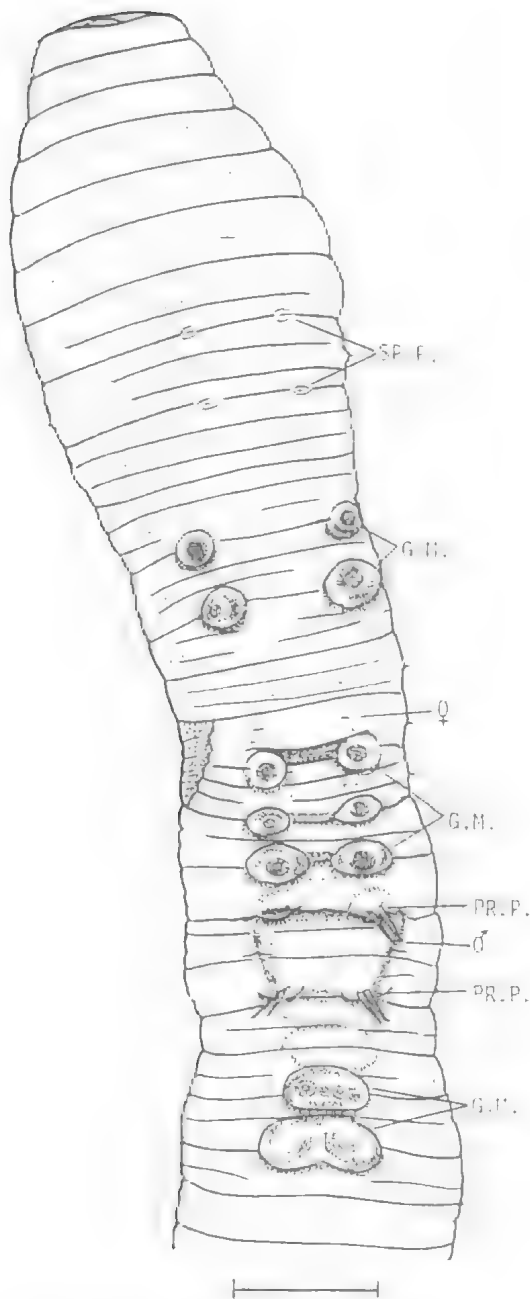


FIG. 3. *Neodiploptrema exigua* genital field.

pigmentless buff in alcohol. Prostomium prolobous; first dorsal pore 11/12 (imperforate). Setae 8 per segment, commencing in II; ventral setal couples of XVIII present; those in XVII and XIX modified as enlarged penial setae; genital setae lacking. nephropores not visible externally.

Clitellum very faint, barely distinguishable. Male pores located presetally, in definite seminal grooves, on XVIII, lateral of *b*-lines. Prostatic porophores 2 pairs, in XVII and XIX, each on a distinct papilla, and intimately associated with (usually) protuberant penial setae. The slightly convex male field is delimited laterally by the seminal grooves (joining the prostatic pores of a side), with the prostatic porophores defining its corners. Female pores small slits presetal in XIV, in *ab*. Spermathecal pores 2 pairs of simple depressions, in 7/8 and 8/9, in *ab*. Accessory markings 2 pairs of rounded tumescences with oculate centres present intersegmentally, in 10/11 and 11/12. A further series of three more closely paired markings (of similar shape) present in 14/15 and 16/17, slightly lateral of *b*-lines; the markings in 14/15 are separated by a distinct depression, the remainder to a much lesser extent; a diffuse and indistinct pad extending from the posterior edge of the male field to the anterior portion of segment XXI is seen to be of width *bb*; 2 further unpaired median markings are located in 21/22 and 22/23, the former the smaller, with a multi-oculate central area, the marking in 22/23 longer, almost paired, with central depressions.

Septa: 5/6 delicate, 6/7-7/8 slightly thickened, 8/9-12/13 moderately muscularised, 13/14 slightly affected, remainder diaphanous. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII, those in X-XIII considerably larger than the remainder, with connectives from both the dorsal and supra-oesophageal vessels; the latter vessel moderately developed, its limits not determinable. Gizzard large, though compressible, in V; oesophagus narrow, VI-XIX, but with three pairs of obvious pouches in XVI-XVIII, that closely resemble stalked calciferous glands; these are complexly vascularised, and contain conspicuous lamellae; the three pouches on each side of the oesophagus are clearly interconnected, but communication of each of the pouches independently to the oesophagus could not be demonstrated. Intestinal origin XX, a robust, though flattened, dorsal typhlosole is present after XXV. Meronephric; the mid-body segments each containing a pair of large megameronephridia with preseptal nephrostomes, their terminal ducts discharging to a pair of ventral, longitudinal ureters that run the entire length of the body, opening at the anus; the megameronephridia decrease gradually in size posteriorly, and disappear abruptly approximately 25 segments from the posterior end; in addition to the above, each intestinal segment contains 3

pairs of small, astomate, exonephric loops, distributed evenly on each side of the nerve-cord, the dorsalmost body just below the mid-dorsal line; these persist (perhaps with some slight trend towards a size increase) to the caudal extremity. A large pair of tufted nephridial bodies is present in V, with a much smaller set in VI.

Holandric; large, iridescent spermatic funnels and sperm masses seen in X and XI; 2 pairs of palmate seminal vesicles composed of large, slightly iridescent loculi present in IX and XII, the former somewhat smaller and compressed. Prostatic glands 2 pairs of simple tubular structures in XVII and XIX, the anterior pair the larger; the ducts are weakly muscular, and short. Penial seta follicles proportionately large for the species, each follicle with a distinct retractor ligament inserted on the dorsolateral aspect of the body wall. The setae fairly flat, gently curving, the ectal region with a distinct sinusoidal bend; the ectal 1/4-1/3 is ornamented with clusters of 1-4 irregular, jagged teeth. Length mature seta 2.4mm; midshaft diameter 53.4µm (mean of 3). Ovaries, comprising several strings of medium-sized oocytes, together with small, pleated oviducal funnels, present in XIII; minute rounded structures on the posterior face of septum 13/14 are questionably ovisacs. Spermathecae rather small, each organ consisting of an ovoid ampulla and sacciform, blunt diverticulum (with some iridescence); duct very short. Length right spermatheca of IX 0.6mm (base of ampulla to pore). Genital seta follicles absent.

ETYMOLOGY. Referring to the distinctive nephridial system.

REMARKS. This small species has undoubted affinities with *N. varionephrica*, both species possessing a remarkable nephridial system which incorporates a combination of micromeronephridia and megameronephridia, the latter with longitudinal ureters. This arrangement (as described in detail above) is reminiscent of that described by Bahl (1942) for the dichogastrin *Hoplochaetella khandalensis*, though in that species, the longitudinal ureters are located dorsally, and the megameronephridia continue to the extreme caudal segments. Bahl, in summarising nephridial modifications in earthworms, describes the condition whereby the common excretory canals open at the junction of the body wall and the gut (i.e., the anus) as 'the first steps, so to speak, in the enteronephric direction' (Bahl (1947). An anatomical arrangement of the excretory system whereby longitudinal ureters termi-

nate in the proctodaeal region is also seen in the Western Australian genus *Austrohoplochaetella* and the African species, *Millsonia anomala*. Jamieson (1974) detected significant intraspecific variation in the occurrence of meronephry in the Tasmanian species *Cryptodrilus polynephricus*, a further indication of the lability of this character-state.

The occurrence of this relatively advanced nephridial system in *Neodiploptrema* raises problems for the existing classification (Jamieson, 1971), in which, by definition, *N. varionephrica* and *N. exigua* would be placed in the Dichogastrini, within a different subfamily to that in which the bulk of *Neodiploptrema* species would be assigned. Apart from the nephridial modifications, which together with the absence of genital setae, serve to distinguish it from its congeners, *N. exigua* is otherwise unremarkable, there being little to justify the erection of a higher taxonomic category (i.e., a subgenus) to accommodate it and *N. varionephrica*.

***Neodiploptrema lacisbrontoi* sp. nov.**  
(Figs 4, 11D)

TYPE LOCALITY. 10°46'S, 142°34'E, dense rainforest at northern end of Lake Bronto, in openings in forest canopy, black sandy soil, dense leaf and twig litter, some ground cover, 1 m deep. Coll. R. Raven, 4 Feb 1975.

MATERIAL EXAMINED. HOLOTYPE. QMG211957. PARATYPE. QMG211958 (4 specimens).

DESCRIPTION. Length 165+, 140mm (Holotype, P1). Width 4.9mm (H). Form circular in cross-section throughout, pigmentless buff in alcohol. Prostomium strongly furrowed. First dorsal pore at 9/10. Setae 8 per segment, closely paired, the ventral setal couples of XVIII absent; those of XVII and XIX modified as enlarged penial setae; the ventral setal couple on the left side of X very slightly enlarged, but cannot be regarded as functional genital setae. Nephropores not visible externally. Clitellum annular, fairly strongly developed over XIII-XVII (P1), setae visible. Male pores are situated just posterior to intersegment 17/18, lateral to *b*-lines; each surmounts a tiny papilla in a distinctly demarcated seminal groove, which connect the porophores on each side. Prostatic openings, 2 pairs, in XVII and XIX, not on distinct papillae, but rather at the anterior rim of small, circular concavities (more pronounced in the anterior pair), which form the four corners of a roughly square male field. In

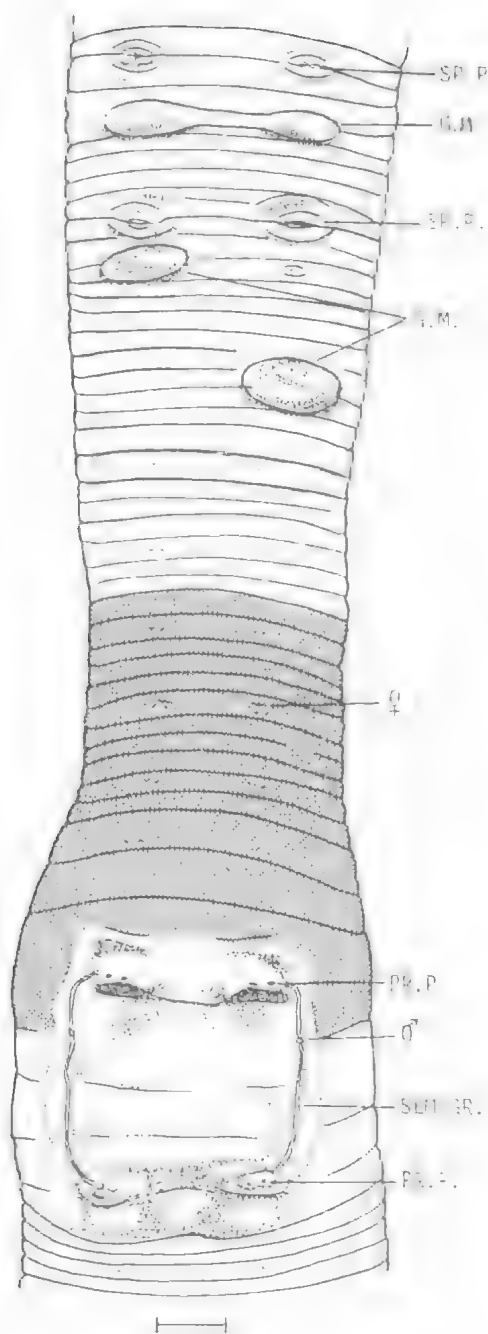


FIG. 4. *Neodiploptrema laevisbrontoi* genital field.

undissected specimens, this region appears slightly depressed with respect to the remainder of the body surface. Female pores are inconspicuous slits slightly pre-setal in *a* of XIV. Sperma-

thecal pores 2 pairs in 7/8, 8/9, each with a conspicuously puckered rim. Accessory markings a very narrow tumid strip in XXI in *aa* with central depression; a similar marking in 20/21 without depression; a large tumescent patch in the upper portion of segment XVI, in *bb*; a papilliform swelling in X, centred on the left side ventral setal couple, but extending laterally in both directions, as well as anteriorad and posteriorad (P1 right side only, P2 present over both setal couples (reduced in size), P3 both sides, P4 right side only; a similar marking in IX, centred on *ab*, but confined within 2 adjacent intrasegmental furrows (H only); a pair of papilliform swellings in VIII, similarly disposed, but (H) conjoined by a median tumid band, P3 small papilla left side only, P4 left side only.

Septum 5/6 moderately thickened, septa 10/11, 11/12 strongly so, 6/7-9/10 very much thickened and muscularised. Dorsal blood vessel single, continuous onto the pharynx, where it divides repeatedly. Last hearts in XIII; those in XII and XIII the only large heart-like commissurals, the remainder being much reduced, and decreasing in size anteriorly; commissurals in X-XIII have thin connectives to both the dorsal and supra-oesophageal vessels; the latter is visible in segments X-XVI only, though ill-defined in segments X and XI. Gizzard very large, cylindrical and highly muscular, though somewhat compressible, in V. Oesophagus narrow, with conspicuous lateral pouching in XIV-XVI (in P1 only present in XIV and XV); these outpouchings are internally lamellate, but their function is conjectural (calciferous, digestive, etc.); a further small dilatation of the oesophagus is present in XIII. Intestine commences with abrupt expansion in XVIII (XVII-P1), a definite double-ridged dorsal typhlosole present from XIX posteriorad, being maximally developed from segment XXX. Nephridial system meronephric, in the forebody consisting of numerous, simple astomate, exonephric loops in each segment (more than 30 in the intestinal region); Caudally (i.e., the last 35-40 segments, the nephridial bodies of the last 15 or so segments being considerably enlarged. No enteronephry demonstrable; tufting present in IV, presumably enteronephric, but the composite ducts not traceable; the nephridial loops noticeably longer in V and the following oesophageal segments than in the intestinal region.

Holandric; 2 pairs small, highly convolute non-iridescent sperm funnels in X and XI, the former the larger; 2 pairs rounded, racemose seminal vesicles in XI and XII, the latter being obviously



the larger; (vice versa in P1). Vasa deferentia readily traceable on the body wall as a pair of closely associated tortuous tubes entering the parietes in XVII. Prostates, 2 pairs in XVII and XIX, each a narrow, highly coiled tube, restricted to its segment of origin, with a long, thick, looped muscular duct; the anterior prostates are invariably the larger pair. Medium-sized penisetal follicles, containing few reserve setae, present in XVII and XIX, associated with the prostatic ducts; extensive copulatory musculature (i.e., connective ligaturing of the follicles to the body wall, for the eversion and/or retraction of the penial setae during copulation) present. The setae robust, stout, somewhat flattened, the ectal end often twisted, the tip invariably recurved; the ectal 1/3 is ornamented with incomplete, staggered circlets of short, irregular toothlets. Length of mature seta 0.88mm; midshaft diameter 31.7µm (mean of 3). Ovaries fan-shaped, consisting of many strings of small oocytes, and these, together with medium-large oviducal funnels, are located in XIII. Spermathecae 2 pairs, in VIII and IX, each comprising a sacciform ampulla that is produced into a long digitiform projection (directed antieriad *in situ*), and a sessile, U-shaped diverticulum studded with large, iridescent, intramural sperm chambers; the diverticulum is embedded in the wall of the sac-like portion of the ampulla; length of right spermatheca of IX 2.9mm. Brain crescentic, with broad fusion of the supra-oesophageal ganglion; 2 quite distinct prostomial nerves arise close together at the point where the commissure widens to form the dorsal ganglion; these innervate different regions of the prostomium. Peristomial nerve single, but branching a short distance from its point of origin at the commissure (approximately midway between the sub- and supra-oesophageal ganglionic masses). Spermathecal genital setae absent; slightly enlarged setae are associated with the genital marking on left IX, but these are not specialised, and appear to be non-functional.

**ETYMOLOGY.** For the type-locality, Lake Brontō.

**REMARKS.** This species is distinguished from other forms in lacking genital setae, in having the male pores in an anterior position (near 17/18), and in exhibiting oesophageal pouching in the region XIV-XVI. Its closest affinities appear to lie with the much larger *N. raveni*, though this relationship is by no means close.

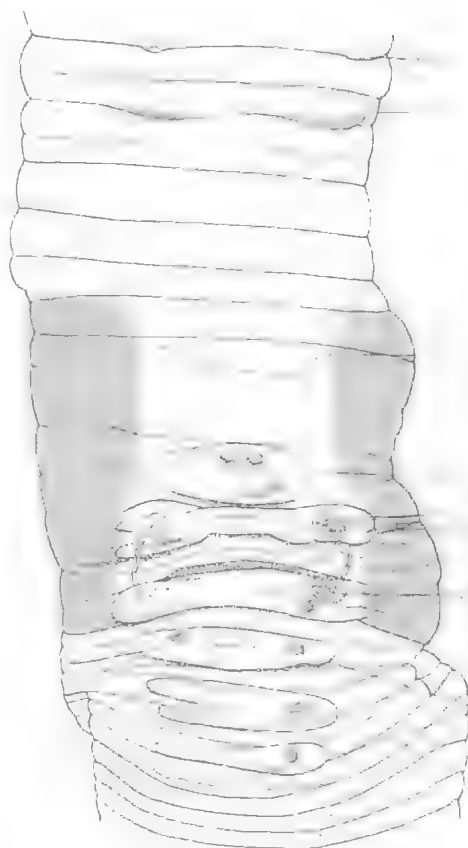


FIG. 5. *Neodiploptrema occidentalis* genital field.

***Neodiploptrema occidentalis* sp. nov.**  
(Figs 5, 11F)

**TYPE LOCALITY.** 12°35'S, 141°55'E, Weipa, north bank of the Mission River, Cape York Peninsula, in semi-deciduous vine-forest, litter layer 4-5cm deep, over black 'bauxite' soil. Coll. R. Raven, 7 Feb 1975.

**MATERIAL EXAMINED.** HOLOTYPE. GD 75/44. PARATYPES. 2 acitellate specimens. GD 75/45.

**DESCRIPTION.** Length 34+ (posterior amputee), 59mm. Width (midclitellar) 4.4, 4.2mm. Segments ?, 135 (Holotype, P1). Circular in cross-section throughout, pigmentless buff in alcohol, preservation poor (some maceration). Prostomium pro-epilobous, first dorsal pore 18/19 (H, P1). Setae 8 per segment, closely paired. Ventral setal couples of XVIII present; those of XVII and XIX enlarged as penial setae; genital

setae lacking. Nephropores not externally recognizable. Clitellum tumid, saddle-shaped, better developed dorsally, extending over segments XIII-XIX, the ventro-lateral limits indefinite. Male pores not definitely demonstrable (due to partial maceration), but presumed to lie within the shallow seminal grooves linking the prostatic pores of a side; the latter are atop tumid mounds that are connected across the ventrum by raised glandular strips. Each prostatic papilla bears 3 conspicuous pores; the two more closely associated openings marking the site of exit of the penial setae (as evidenced by the occasional protruding seta), whilst the remaining orifice is the prostatic opening proper. Female pores a pair of obvious slits close to seta *b* in XIV. Spermathecal pores inconspicuous in 7/8 and 8/9, aligned with *ab*. Accessory markings a series of single, median pads with paired pore-like centres; a marking in XVI, with the oculate dimpling closely paired, in the setal arc; a set of markings decreasing in lateral width posteriad, commences in XIX, immediately posterior to the prostatic porophores (confluent with the tumid strip linking the latter), and extends to XXII, the eye-like margins widely-spaced, not always present on the right side; a further slight swelling is present medially in XXIII. The small protruberances in VIII, which overhand the spermathecal pores are apparently not associated with genital seta follicles.

Septa 5/6 diaphanous, 6/7 slightly thickened, 7/8-9/10 moderately thus, remainder delicate. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII, these commissurals being the only ones of any significant size, though those in XII are fairly robust; commissurals in XI-XIII demonstrably latero-oesophageal, with the supra-oesophageal vessel visible in segments X-XIII only. Gizzard large and firm, dolioform, in 5/6; oesophagus narrow, its length partially restricted by the posteriorly transgressive gizzard; intestine commences in XVI, no definite typhlosome noted. Meronephric throughout; a pair of very large tufts present in III, their composite ducts running anteriorly to discharge into the buccal cavity; in the mid-body, each segment possesses approximately 10/12 scattered astomate, exonephric loops; caudally, the medianmost nephridium is enlarged as a megameronephridium (on each side), having a large, preseptal nephrostome; its ducts were not traceable owing to poor fixation; the remaining nephridia are smaller, astomate, and reduced in number (apparently only 3 on each side, regularly spaced).

Metandric; a single pair of faintly iridescent spermathecal funnels that are nonetheless quite large, together with presumed testicular tissue (attached to posterior face of septum 10/11), seen in XI; the funnels are situated on septum 11/12, above the ventral body wall, with the vasa deferentia running down the septum and onto the peritoneum, where they are traceable as single, lazily winding ducts. A single large pair of seminal vesicles that are finely racemose are located in XII. Prostatic glands 2 pairs of very thin, flattened tubes, restricted to XVII and XIX, the anterior pair obviously the larger; the ducts are straight and poorly muscularised. Large, conjoined penial follicles containing numerous reserve setae, are associated with the ectal portion of the prostatic glands and their ducts; copulatory musculature is reduced to thin ligaments; the setae gently curving, tapering gradually to a rather blunt tip; the ectal extremity (approx. 1/5) ornamented with incomplete rows of very short, jagged toothlets, which become sparser proximally. Length of mature seta 1.63mm; midshaft diameter 34.2µm (mean of 2). Ovaries small, with minute funnels, in XIII, ovisacs not seen. Spermathecae 2 subequal pairs, in VIII and IX, each consisting of a bent, tubular ampulla, and sessile, reniform diverticulum, with 2 radially arranged intramural sperm chambers containing innumerable brightly iridescent flecks. Length right spermatheca of IX 1.2mm (base of ampulla to pore).

**ETYMOLOGY.** For the type-locality at the western extremity of the known generic distribution.

**REMARKS.** The metandric condition of the male gonads, and the lack of genital setae, together with certain nephridial peculiarities, serve to characterise *N. occidentalis*. It is not known whether this species is linked through intermediate populations to the Lockerbie and Iron Range endemics, or is an interpluvial isolate. Semi-deciduous notophyll vine-thickets are very restricted in the Weipa region, usually located on well-drained sites where freshwater aquifers are close to the surface; if *N. occidentalis* is an obligate closed forest inhabitant, its range must necessarily be strictly limited.

***Neodiploptrema raveni* sp. nov.**  
(Figs 6, 11G)

**TYPE LOCALITY.** 10°48'S, 142°28'E. Lockerbie East, Cape York Peninsula, collected through formalin expulsion of very rocky, red lateritic soil; Coll. R. Raven, 2 Feb 1975.

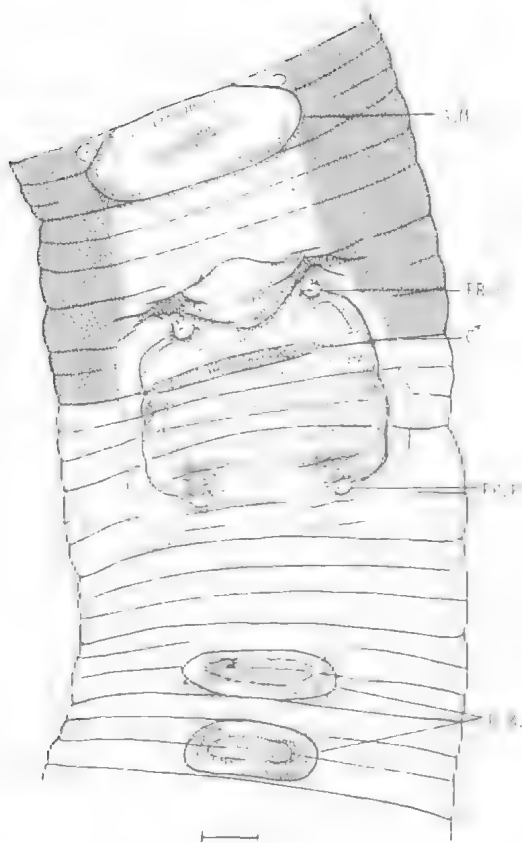


FIG. 6. *Neodiploptrema raveni* genital field.

**MATERIAL EXAMINED.** HOLOTYPE. QMGH2951  
PARATYPES. Paratypes 1 and 3 QMG211959;  
paratypes 2 and 4, ANIC GD 95,9,4

**DESCRIPTION.** Length 465, 398mm. Width (midclitellar) 9.0mm, 6.8mm. Segments 457, 499 (H, P1). Circular in cross-section, pigmentless biscuit in alcohol. Prostomium pro-epilobous, peristomium much fissured. First dorsal pore 10/11 (H), 9/10 (P1, 4). Setae 8 per segment, in regular longitudinal rows throughout; ventral seta couples of XVIII present; those of XVII and XIX modified as enlarged penial setae; those of IX replaced by genital setae. Nephropores not seen. Clitellum saddle-shaped, weakly developed, over 1/2XII-XVII. Male pores inconspicuous, in the seminal grooves at 17/18, well lateral of *b*-lines; prostatic pores 2 pairs, in XVII and XIX, coincident with the penial seta orifices, on distinct mounds; the seminal grooves joining the pores of a side are very narrow, but deep, and are slightly convex laterally. The porophores lie in four dis-

tinctly sunken areas, which are transversely linked by two fairly broad channels, in XVII and XIX, the former of which is interrupted by a prominent cuneate tumescence in 16/17. The male genital area, bounded by the seminal grooves and the above-mentioned depressions, is concave with respect to the remainder of the body surface. Female pores inconspicuous openings well ventral of *a*, near 13/14. Spermathecal pores considerable, but located in deep intersegmental grooves, in 7/8 and 8/9, in *ab*. Accessory markings extensive torose tissue associated with the genital setae, in IX, forming a characteristic dumbbell-shaped tumid area (all specimens); a broad, pad present in X (H, P1-2), occasionally a similar marking in XI (P2); a series of elliptical pad-like markings (extending across *bb*) with transversely depressed centres seen in XXI (H - the smallest of the three markings), in XXII (H, P1/3, P2 - indistinct), and in XXIII (H, P1, P2 - indistinct); a broad pad, occupying much of the longitudinal dimension of XV, extends across *bb* (H, P1-2).

Septa: 5/6 moderately thickened, 6/7-10/11 much augmented with thick musculature (7/8-10/11 the strongest), 12/13 slightly thickened, remainder delicate. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII, only the commissurals in XI-XIII large, heart-like, and receiving connectives from both the dorsal and supra-oesophageal vessels. The latter connectives are the more substantial; the supra-oesophageal vessel was noted in segments X-XIII only. Gizzard enormous, cylindrical, and virtually incompressible, in V; oesophagus completely suppressed by the posteriad encroachment of the gizzard in VI-X; thereafter highly vascular, but lacking pouching or calciferous glands. Intestine commences in XVIII, a strong dorsal typhlosome beginning abruptly at XIX. Meronephric throughout, nephridia commencing in II; very conspicuous, profusely divided tufts present in III and IV, their composite ducts running anteriorly, but not traced. The oesophageal region with large numbers of astomate, exonephric, sessile loops restricted to the parietes or the septal bases; these are fewer in number in the intestinal region, with a distinct concentration of bodies near the ventral nerve-cord; caudally, there is a multiplication and enlargement of the nephridial bodies, each apparently with its own preseptal nephrostome.

Holandric; wispy testis material and small-medium spermatic funnels (diaphanous, translucent?non-functional) present in X and XI, testis-sacs absent; large, acinous, very finely divided semi-

nal vesicles present in XI and XII, the latter mass the larger. Prostatic glands 2 pairs of simple tubular organs restricted to, and extending laterally in, their segments of origin; the anterior pair is the larger. Each gland possesses a fairly long, coiled, muscular duct. The *a* and *b* follicles of the penial setae are indistinguishable, forming 2 pairs of stout, strongly curved bundles joined to the body wall in a number of places by copulatory ligaments. The setae broad, flattened, attenuating abruptly near the ectal end, the ectal extremity invariably recurved; the shaft with a faint scattering of very fine clusters of short toothlets distally. Length of mature seta 3.43mm; midshaft diameter 123.9 $\mu$ m (mean of 2). Medium-sized, pleated oviducal funnels seen in XIII, small ?ovisacs attached to the posterior face of septum 12/13. Spermathecae 2 pairs, in VIII and IX, each organ consisting of a rounded diverticulum sessile on the body wall (duct virtually non-existent), and a regular, ovoid ampulla connected to the latter by a distinct, narrow peduncle; length right spermatheca of IX 3.8mm. Genital seta follicles a single pair, in IX, each containing several yellowish, slightly curved setae; these are ornamented over their ectal 1/3 not with scalloping, but with irregular transverse dentate grooves that are at the most 1/3 shaft circumference long. Length of mature seta 2.77mm; midshaft diameter 79.5 $\mu$ m (mean of 3).

ETYMOLOGY. For the collector, Robert Raven.

REMARKS. The lack of spermatozoal iridescence in the spermathecae or testis-segments in any of the specimens examined points to a parthenogenetic mode of reproduction for the species. *N. raveni* is a very large, deep-burrowing, distinctive species which is very readily identified, even in a comparatively juvenile state because of the peculiar bipartite spermathecae. It possibly also exists in the Torres Strait Islands in suitable habitats, but because of its burrowing habits, it would not be readily collected.

***Neodiploptrema tumida* sp. nov.**  
(Figs 7-8, 11E,H)

TYPELOCALITY. ca. 10°48'S, 142°28'E, Lockerbie East, Cape York Peninsula, Coll. R. Raven. Holotype and paratypes 1, 3, 4; 2 Feb 1975; paratypes 5 and 6; 30 Jan 1975; paratypes 7-10, 11-17; 1 Feb 1975; paratypes 10, 18, 19; 3 Feb 1975.

10°35'S, 142°13'E, Green Hill, Thursday Island, in damp black clayey soil between rocks in vine-forest, paratypes 20-25, Coll. G. Berry, 7 Dec 1975.

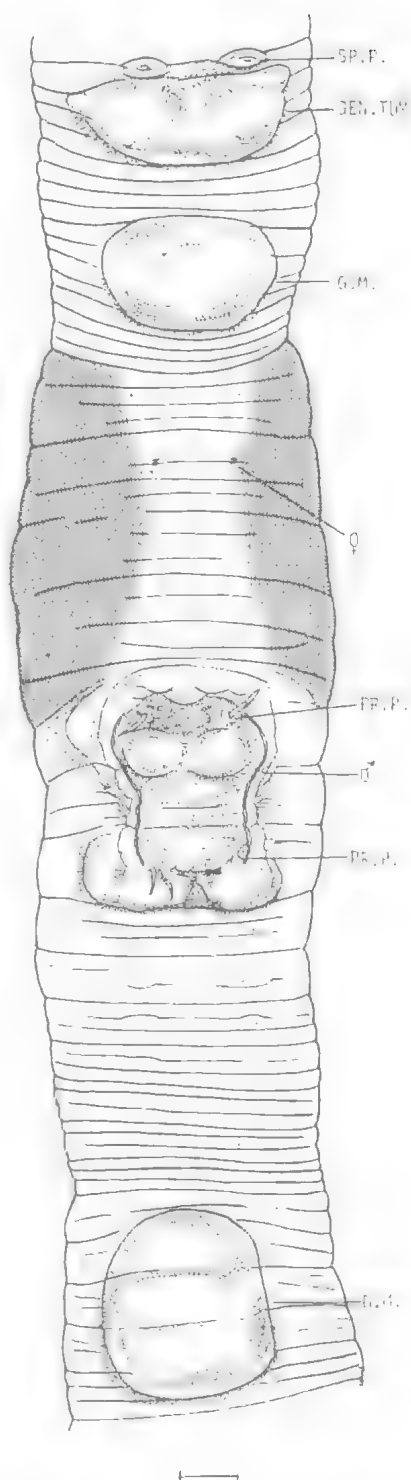


FIG. 7. *Neodiploptrema tumida* genital field.

MATERIAL EXAMINED. HOLOTYPE. ANIC GD.95.9.8. PARATYPES. P1, P3, P4, ANIC GD.95.9.8; P5-6, ANIC GD.95.9.6; P11-13; P14, ANIC GD.95.9.7; P10, P18 & P19 (desiccated) ANIC GD.95.9.9.

DESCRIPTION. Length 149, 142.5mm. Width (midclitellar) 4.5, 3.4mm. Segments 282, 242 (Holotype, P1). Form circular in cross-section throughout, pigmentless buff in alcohol, clitellum in some specimens pink (P2, P4-6). Prostomium prolobous; first dorsal pore 8/9 (H, P1-2, P4) or 9/10 (P3). Setae 8 per segment, in regular rows throughout; ventral setal couples of XVIII absent; those in XVII and XIX modified as penial setae; those of IX as genital setae. Nephropores not conspicuous. Clitellum strongly-developed, saddle-shaped, over XIII-XVI (H, P1, P2-4); dorsal pores and intersegmental furrows distinct, setae obscured. Male pores slightly presetal, in narrow but deep seminal grooves that link the prostatic pores of a side; the latter are located in lateral depressions, separated by a central cuneiform tumescence; the posterior margins of the depressions in XVII and XIX are filled with 2 pairs of large, rounded swellings (anterior pair the larger), extending laterally to the seminal grooves, slightly beyond *b*-lines; segment XVIII slightly raised and traversed by deep intrasegmental furrows, and longitudinally seminal grooves, which turn ventrally to *b*-lines in XVIII. Female pores inconspicuous in a transverse furrow, just median of *a*-lines near intersegment 13/14, in XIV. Spermathecal pores very obvious on protuberant lips in *b*-lines, in 7/8 and 8/9. Accessory markings, a very large, swollen mound filling segment XI between the intersegmental furrows, and extending laterally beyond *b*-lines by a distance approximately equal to  $2bc$  (all specimens); a similar tumescence extends over 3 segments (XXVIII-XXX), with some encroachment on segments XXVII and XXI; it is dissected by the intersegmental furrows of the segments it occupies (see thus in H, P7); XXVIII-XXIX only in P4, P8; XXIX-XXX only in P1, P2, P5-6, P9, P16, P17, P18); XXX-XXXI only in P3; a swollen mound associated with genital setae in IX, with similar proportions to the accessory markings in XI (H, P1-19). Accessory marking in XXXII only (P12, P15, P19); XXVIII-XXIX only (P13); XXIX-XXX only (P11); XXXI-1/2XXXII only (P10); XXIX-1/2XXXI only (P14).

Septa 11/12 moderately, 6/7-10/11 strongly muscularised, 5/6 only slightly thickened. Dorsal blood vessel single, continuous onto pharynx, where it divides repeatedly in III and IV. Supra-

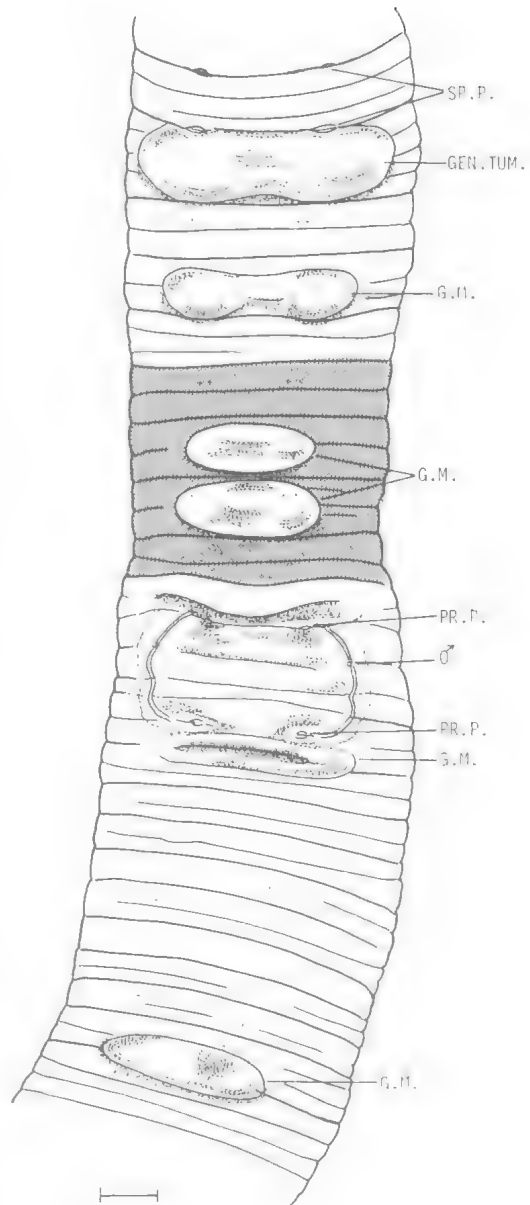


FIG. 8. *Neodiploptrema tunida* genital field.

oesophageal vessel present, 1/2XI-XIV. Last hearts in XIII; those in XI-XIII the largest, receiving connectives from dorsal and supra-oesophageal vessels, the latter sending the larger connectives in XII and XXIII; the remaining commissurals decreasing in size anteriorly, and dorsoventral only. Gizzard large, highly muscular, and barrel-shaped, in V, with conspicuous

midlength furrow. Oesophagus rather wide, thin-walled, in VI-XVI, vascularised to any extent only in XI-XVI; calciferous glands or pouching absent. Intestine commencing in XVII, with a low dorsal typhlosole commencing early, well-developed by XXV. Metanephric throughout; the pre-intestinal region with scattered astomate exonephric loops adherent to the body wall and septa, becoming more numerous in the intestinal region posteriad of XV (here the nephridial bodies are attached exclusively to the body wall); caudally with slight enlargement of the nephridial bodies each with a conspicuous pre-septal nephrostome (at least 8 counted on each side); robust pharyngeal tufting present in III and IV, the composite ducts not traced.

Holandric; small, iridescent, compactly plicate funnels and compacted sperm masses present in X and XI; loosely packed seminal vesicles with small, scattered loculi present in XI and XII. Prostatic glands small, flattened, tightly coiled tubular organs with origins in XVII and XIX, the latter pair much reduced (?becoming vestigial); a very long, coiled, muscular duct enters a lobulate glandular mass on each side in XVII, but these enter the parietes directly in XIX. Penisetae follicles conspicuous, and attached by ligaments to the body wall in XVII, the bundles reduced in size in XIX; the setae are fairly long, and bent into an arc; the distal portion is often twisted with respect to the main axis of the seta, the extreme ectal tip is invariably sharply recurved, uniform, the immediately posteriad portion of the shaft obviously thickened; the ectal of the shaft is ornamented with short, discontinuous rows of fine teeth, the rows arranged in a crude alternation. Length of mature seta 2.29mm; midshaft diameter 77.0µm (mean of 2). Small ovaries, and medium-sized plicate funnels seen in XIII, ovisacs (?) attached to the posterior face of septum 12/13. Spermathecae 2 pairs in VIII and IX, the posterior pair readily perceived as the larger; each organ consists of a large, ovoid, bipartite ampulla, and a flattened, sessile, multi-loculate diverticulum occupying the dorsal aspect of the smaller ampullal portion; duct extremely short; length of right spermatheca of IX 2.7mm. A pair of small genital seta follicles present in IX (directed anteriorly, lying beneath the spermathecae); specialised glands lacking; the setae fairly straight, the ectal 1/5 distinctly ornamented with deep notching, the proximal rims of which are armed with irregular, sharp, triangular teeth. Length of mature seta 2.29mm; midshaft diameter 52.4µm (mean of 3).

ETYMOLOGY. For the large ventral genital tumescences.

REMARKS. The Thursday Island specimens differ in a number of respects from the Lockerbie forms, almost to the extent that subspecific rank might be warranted. There are, however, unusual morphological features common to both that signify close relationship. The major divergences from the type description exhibited by the Thursday Island forms are as follows: Length 140-175mm; width (midclitellar) 4.4-4.7mm; segments 313-324; first dorsal pore 9/10-11/12. Accessory markings a large, tumid pad extending across cc, and filling segment IX longitudinally (P20-21); a pair of mounds or composite bigartite tumescences post-setally in XI, extending laterally to mid-*bc* (P20-21) and XV (P20-P21); a large, median tumid pad occupying most of segment XXVIII and the extreme anterior portion of XXIX (P20-21). Supra-oesophageal vessel seen in X-XVI; intestine commences in XIX; typhlosole commences immediately, but enlarges abruptly in XXXI as a complex, 4-folded structure; posterior prostatic glands not much reduced (as for mainland specimens); spermathecal ampulla bent, slightly bulbous ectally, the diverticulum a sessile tubercle on the bulbous portion of the ampulla. Length right spermatheca of IX (base of ampulla to pore 2.6mm).

The presence of genital setae in IX, the location of the male pores in 17/18, the occurrence of a large genital pad in the vicinity of XXVIII-XXXI, and the terminally bulbous, hooked penial setae are all characteristic of *N. tumida*, and may be used in combination to confirm identity. Immature material from Horn Island may also be referable to this species, a further indication that it is comparatively widespread. Little divergence has apparently occurred since the presumed separation of the mainland from Thursday Island populations after the drowning of Torres Strait, approximately 6,500-8,000 years bp. The duration of insular isolation is approximately equivalent to that experienced by mainland and Melville Island populations of *Diplotrema ridei* in the Northern Territory, though overall morphological divergence is slightly more pronounced in the latter case.

*Neodiplotrema varionephrica* sp. nov.  
(Fig. 9)

TYPE LOCALITY. 10°46'S, 142°34'E, Eastern side of Lake Broote, approximately 10 km from the tip of Cape York Peninsula, in dark sandy soil in open *Eucalyptus*.

*Lyptus* dominated forest, with dense ground cover. Coll. R. Raven, 2 Feb 1975.

**MATERIAL EXAMINED.** HOLOTYPE. QMGH2952. PARATYPES. QMGH2953. OTHER MATERIAL. Lake Bronto, on eastern side of lake, open eucalypt forest, much ground cover, dark sandy soil. One specimen registered as QMG211960; 11 further specimens registered as QMG211961.

**DESCRIPTION.** Length 43, 42+ mm (posterior amputee). Width (midclitellar) 3.1, 3.0 mm. Segments 155, 110+ (Holotype, P1). Form circular in cross-section throughout, pigmentless grey-buff in alcohol, clitellum a slight pinkish-brown. First dorsal pore 11/12 (H, P1), prostomium propilobous. Setae 8 per segment, commencing in II, in regular longitudinal rows throughout; ventral couples of XVIII absent or much reduced; those of XVII and XIX modified as enlarged penial setae; those of X replaced by genital setae. Nephropores not visible externally. Clitellum annular, more pronounced dorsally, over XIII-XVIII; dorsal pores obscured, intersegmental furrows only visible ventrally. Male pores small slits located in the relatively broad seminal grooves linking the porophores of a side; the male openings are well lateral of *b*-lines, located approximately midway between the setal arc and 17/18; prostatic pores 2 pairs, in XVII and XIX, each on a slight protruberance overhanging a deep transverse fissure. Female pores small slits barely presetal, median of *a*-lines by the distance *ab* 1 in XIV. Spermathecal pores in 7/8 and 8/9, in *a*-lines, the slit-like pores inclined at a slight angle to the plane of the intersegmental furrows. Accessory markings a conspicuous tumescence associated with the genital setae present in X (H, P1-left side only, P2 left side only). A series of 6 pairs of ellipsoidal intersegmental markings with oculate centres commencing in 10/11 (H, P1-right side only, P2, P3-left side only, P4-11), in 11/12 (H, P1-11), in 12/13 (H, P5-right, P6-right, P9, P11), in 13/14 (H, P1-7, P9-11), in 14/15 (H, P1-5, P6-right, P7-11), in 15/16 (H, P1-10) and in 16/17 (H, P1-11). A broader tumid pad extends laterally to *b*-lines to fill segment XIV between the intersegmental markings at 13/14 and 14/15 (H, P1-2, P3-weak, P4-11); a similar transverse marking may be present in XX (to *b*-lines) seen in P3-4, P7, P9 (weak), P10-11; a transversely elliptical pad in 21/22, extending laterally to slightly beyond *b*-lines is often present (H, P5-6, P10-11), with a similar marking less commonly occurring in 22/23 (P6-7 only); exceptionally, there is an additional marking similar to those in the clitellar region in 20/21 (P10, right side only).

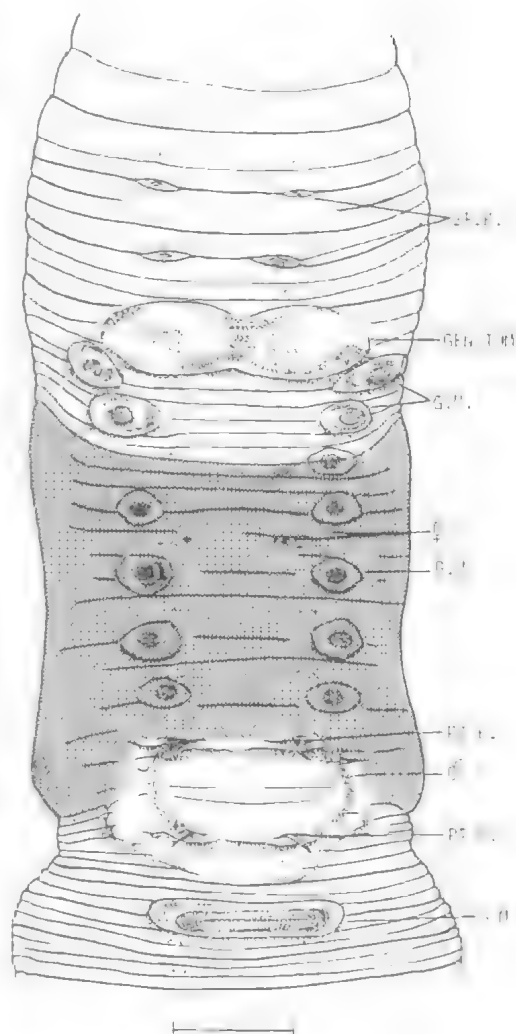


FIG. 9. *Neodiploptrema varioneprica* genital field.

Genital seta location variations: located in VII (P3, left side only, P8, left side only), in VIII (P4-5), and in IX (P3, left side only). No accessory markings corresponding to genital seta locations were detected in P5-7, P9-11.

No septa strongly muscularised, but 6/7-10/11 slightly thicker than the remainder. Dorsal blood vessel single; last hearts in XIII, those in X-XIII with thin connectives received from the dorsal and supra-oesophageal vessels; the latter vessel is detectable in IX-XIII. Gizzard large, well-developed, though compressible, in V, with a softer proventricular portion; oesophagus fairly short, somewhat compressed due to the posterior transgression of the gizzard (septa to 12/13 directed



posteriad as a result of the latter); oesophagus well vascularised, with conspicuous rugae on its inner walls; 3 pairs of large, lateral outpouchings present in XVI-XVIII, containing definite lamellae, but all interconnected, with a single narrow opening leading to the oesophagus proper in XVII. Intestinal origin at posterior end of XVIII, a strongly developed dorsal typhlosole commencing in XXIV. Meronephric; large tufts developed in V, their composite ducts passing anteriorly to the buccal cavity; smaller clusters of loops seen in IV and ?III; the oesophageal region with approximately 6 small astomate, exonephric loops on each side; in segment XX, a conspicuous megameronephridium developed on each side, with a large preseptal nephrostome, and long excretory duct discharging into a thin-walled ureter running the length of the body on either side of the ventral nerve-cord, in *ab*; in addition, 3 small micromeronephridial loops are retained on each side of a segment: one in *bc*, with minute ducts entering the parietes in *b*-lines, an intermediate lateral loop above *d*, and a dorsal body close to the middorsal line (the latter are all astomate and exonephric); this arrangement persists to the extreme caudal segments, the ureters apparently discharging at the anus; the megameronephridia are lost some 30 segments from the posterior end.

Holandric; compacted sperm masses and medium-sized iridescent funnels seen in X and XI; 2 pairs of seminal vesicles, consisting of large, loosely associated loculi, present in IX and XII, the posterior set much larger. Prostatic glands 2 pairs of relatively small, simple tubular structures with short, muscular ducts, restricted to XVII and XIX; penisetal follicles rather small, but densely packed with reserve setae; a single band-like ligature passes across the prostates to link the follicles to the body wall near the mid-dorsal line. The setae gently curving, the tip invariably with a very distinctive trilobate appearance, the ectal 1/4 of the shaft bearing an irregular scattering of thorn-like (slightly recurved) spines. Length of mature seta 1.04mm; midshaft diameter 44.3µm (mean of 3). Ovaries consist of flabelliform clusters of oocytes; these and medium-large oviducal funnels are present in XIII; no ovisacs seen. Spermathecae consisting of an ovoid ampulla and a short, blunt diverticulum containing a number of iridescent intramural pockets. Length right spermatheca of IX 1.2mm. Genital seta follicles usually located in IX, no glandular structures associated; the follicles have some copulatory musculature; the setae are fairly straight, or-

namented over the ectal 1/2-1/3 with regular notching.

ETYMOLOGY. Referring to the highly diverse nephridial system.

REMARKS. This species is closely allied to *N. exigua*, the major synapomorphic character being the peculiar nephridial arrangement (mixed mega- and micromeronephridia in the mid-body, with ureters). *N. varionephrica* may be distinguished on the basis of its very distinctive penial setae, which, unlike any known Australian acanthodrilids, possess trifid tips. Other somatic characters, such as the position of the first intestinal segment, and the presence or absence of genital setae may also be used in conjunction with penial seta morphology to identify the species.

#### Genus *Torresiella* nov.

DIAGNOSIS. Setae eight per segment, prostates a single pair in XIX; male pores a single pair combined with the latter, on XIX. Spermathecal pores a single pair, ventrolateral, in 7/8. Wholly meronephric, with astomate exonephric nephridia throughout; tufting present in the pharyngeal region. Gizzard well-developed, in V. Calciferous glands absent. Holandric, testis-sacs absent. Penial setae and genital setae present.

DESCRIPTION. As for the type-species.

TYPE-SPECIES. *T. singularis* (monotypic).

ETYMOLOGY. Referring to the type locality in Torres Strait.

#### *Torresiella singularis* sp. nov. Dyne (Figs 10, 11A)

TYPE LOCALITY. 10°37'S, 42°17'E, Horn Island, Torres Strait, 0.4km east of the airstrip, in moist clay near eucalypts, beside a narrow creek. Coll. R. Raven, 27 Jan 1975.

MATERIAL EXAMINED. HOLOTYPE. QMGH2936. PARATYPE. QMGH2937.

DESCRIPTION. Length 74, 92mm. Width (mid-clitellar) 3.4, 3.3mm. Segments 164, 202 (approximate due to maceration). Uniformly circular in cross-section, pigmentless grey in alcohol. Prostomium prolobous, peristomium with a dorsal cleft. First dorsal pore 8/9. Setae 8 per segment, commencing in II; caudal setae conspicuously enlarged with respect to the other somatic setae; ventral setal couples of XIX modified as enlarged penial setae; those of XVII and

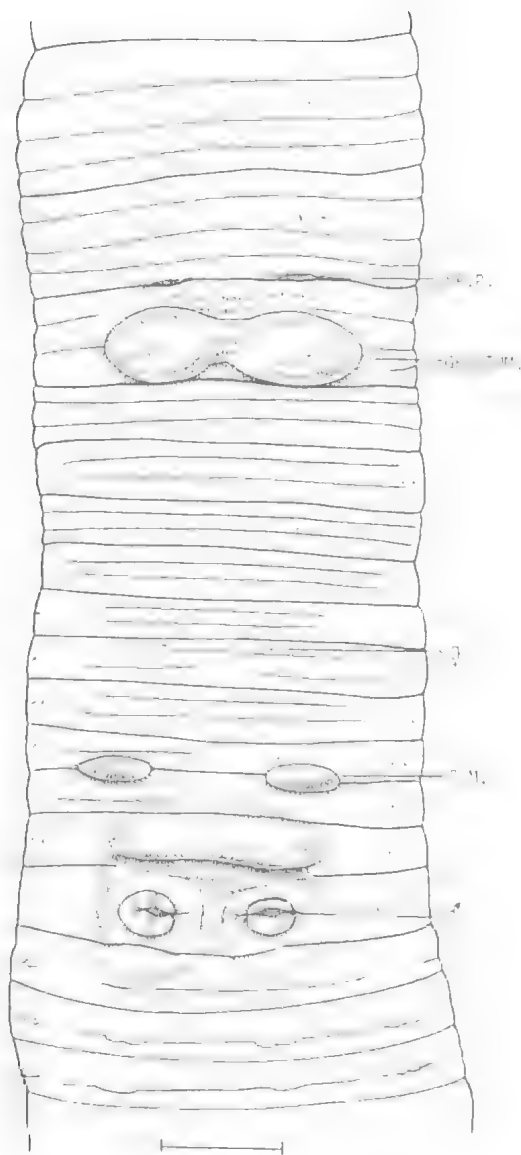


FIG. 10. *Torresiella singularis* genital field.

XVIII lacking. Nephropores not externally recognizable. Clitellum not developed. Combined male and prostatic pores in *ab* on XIX, coincident with the penial seta orifices. The combined pores are located on low mounds, the anterior and posterior approaches of which have a darker, glandular appearance; the male field generally depresses, with a conspicuous furrow at 18/19, overhung anteriorly by a lightly tumid region

across *bb*. Accessory markings slight tumid swelling associated with the development of genital setae usually present in VIII, below the spermathecal pores. Female pores minute points presetally, in an intrasegmental furrow, median of *a*-lines, in XIV. Spermathecal pores a single pair, in *ab*, in 7/8, conspicuous as expanded, rimless orifices.

Septa: 5/6 delicate, 6/7, 7/8, 8/9 with a slight-moderate thickening, 9/10-10/11 moderately muscularised, 11/12 slightly so. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII, those in X-XIII larger than the more anterior commissurals, and with connectives to both the dorsal and supra-oesophageal vessels (the remainder dorsoventral only); supra-oesophageal vessel weakly developed, widest in XIV, not traceable anterior of VIII. Gizzard moderately large, muscular, dolioform, compressible, in V; oesophagus in VI-XVI, fairly wide, well supplied with blood vessels, dilating slightly intrasegmentally; expanded into broad out-pouchings in XIII-XIV, not demarcated from the lumen, or calciferous gland-like. Intestine commences with gradual expansion in XVII, a strongly developed dorsal typhlosole present after XXV. Meronephric throughout; numerous, scattered, astomate, exonephric loops present on the parietes throughout, more numerous in the intestinal region. Caudally, with some slight increase in size, but with no evidence of nephrostomes or enteronephric development. A small tuft occurs in IV.

Holandric; 2 pairs of small, slightly iridescent spermathecal funnels in X and XI, with 2 pairs of small, loosely compacted seminal vesicles in IX and XII; vasa deferentia non-iridescent, clearly visible only in the 3 segments immediately preceding the prostatic segment; still paired on each side in XVIII, fusing in XIX, and entering the parietes simultaneously with the prostatic duct, ?fusing with the latter at this point. Prostatic glands small organs, situated far laterally in XIX, extending into XX, with a few loose coils in the horizontal plane; the muscular duct of uniform diameter, long and straight, perhaps as long or longer than the uncoiled glandular portion, entering the parietes in XIX, through a glandular mass. Penial seta follicles conspicuous, *a* and *b* components distinguishable, each with only 2-3 yellowish setae; the follicles are attached to the body wall by a large band of retractor musculature passing across the prostatic glands, and attached by several strands in 20/21. The setae with a very straight shaft, ectally with a characteristic unci-

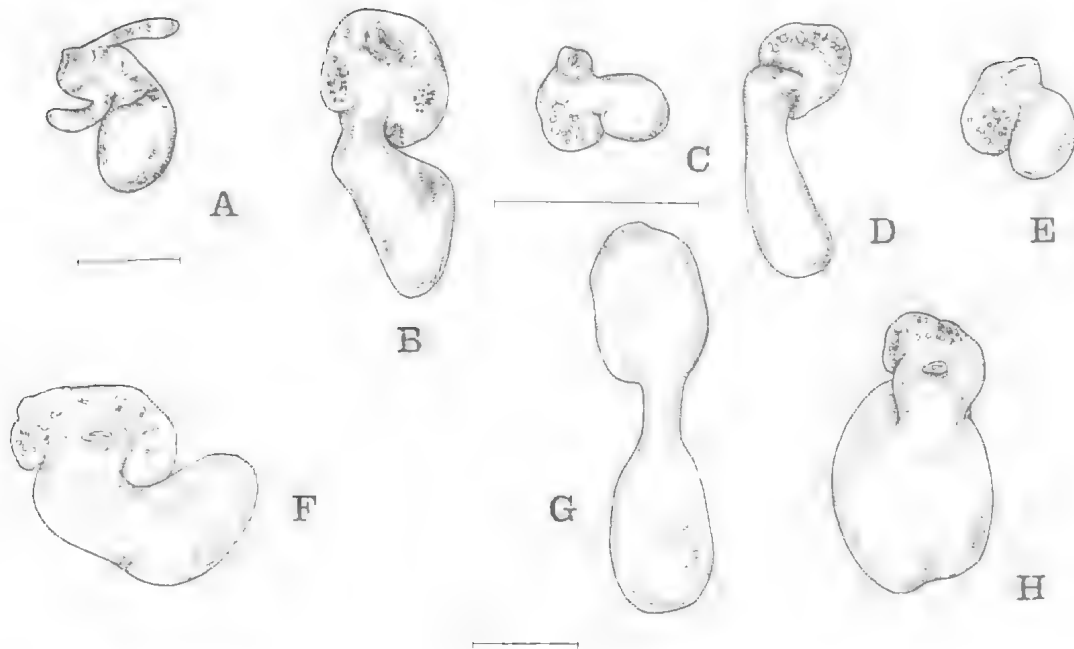


FIG. 11. A, Spermatheca of *Torresiella singularis*. B, Spermatheca of *Neodiploptrema deminutionis*. C, Spermatheca of *Neodiploptrema exigua*. D, Spermatheca of *Neodiploptrema lucisbronti*. E, Spermatheca of *Neodiploptrema varionephrica*. F, Spermatheca of *Neodiploptrema occidentalis*. G, Spermatheca of *Neodiploptrema raveni*. H, Spermatheca of *Neodiploptrema tumida*.

nate appearance; ornamentation restricted to a small region behind the point where the shaft begins to curve sharply, consisting of densely packed, short clusters of jagged teeth. Ovaries small, the ovarian funnels diaphanous, medium-sized, located in XIII; a pair of botryoidal ovisacs present, attached to the posterior face of septum 13/14. Spermathecae a single pair, in VIII, each consisting of a pyriform ampulla, divided into 2 sections by a transverse constriction, and two discrete, clavate diverticula joining the ectal ampullal region; duct indistinguishable from the latter. Length of right spermatheca 2.1mm (the diverticula may be terminally bifid). Genital seta follicles present in VIII, with attached musculature, but no glandular structures. The setae angular in cross-section, fairly straight, the ectal 1/2-1/3 of the shaft conspicuously ornamented with dentate notching.

**ETYMOLOGY.** Referring to the monotypic nature and the rare balantine condition of the genus.

**REMARKS.** *T. singularis* is the only known balantine Australian acanthodril.

## DISCUSSION

*Neodiploptrema* contains species with nephridial systems that by previous definition — having a pair of stomate meronephridia median to astomate micromeronephridia caudally — would be considered to place it in the Dichogastrini, in the subfamily Megascolecinae. The genus is here excluded from the Dichogastrini because of the obvious independent origin of its excretory apomorphy, as evidenced by the undoubted close relationship of its species to those of the holonephric genus *Diploptrema*, in the subfamily Acanthodrilinae (Tribe Acanthodrilini). The classificatory problem raised by the convergent development of complex meronephric systems in the Acanthodrilini (sensu Jamieson, 1971) demonstrated in this paper will need to be addressed more broadly, with particular attention given to the validity of the Dichogastrini as a grouping. Jamieson (1978) has already shown, in a cladistic analysis, that *Dichogaster* (Dichogastrini) grouped with a meronephric *Diploptrema* sp. (now *Neodiploptrema*; Acanthodrilinae) and stated that this grouping tended to confirm his suspicion that

'those *Dichogastrini* with *acanthodrilin* male pores (India and Africa) are descended from *Acanthodrilinae* and are distinct from *dichogastrins* with *megascolecine* male pores (Oriental and Australia)'.

*Torresiella* is also meronephric and appears to be related to the *Diplotrema-Neodiplotrema* assemblage. Balantine reduction (male pores migrating posteriorly to unite with a single pair of prostatic pores, in XIX), which distinguishes *Torresiella* from all other Australian acanthodrilids, is a much less common phenomenon than is the microscolecine transformation (male pores migrating forwards to unite with a single pair of prostatic pores, in XVII). The term derives from a meronephric West African species described by Michaelsen in 1898 for which he erected a new genus, *Balanta*. This was on the basis of the combined male and prostatic pores being located on XIX, an arrangement that had not previously been recorded. Only two years later, in 'Das Tierreich', Michaelsen (1900) suppressed *Balanta* in *Dichogaster*, as its only species, *B. ehrhardti*, had close apparent affinities to other members of that genus, despite the acanthodrilid apparatus of the latter.

Other balantine genera include *Balanteodrilus* (monotypic) recorded from Yucatan Caves by Pickford (1938), and *Sylvodrilus*, a New Zealand taxon. Partial balantine reduction is known from *Udeina* (*U. montanus*) and *Pickfordia* (*P. hemibalantina* Onofredo, 1958); in these species, the posterior prostates are retained, but the male pore has not migrated, remaining in XVIII. In *Sylvodrilus*, the male pores have shifted to the posterior part of XVIII, and in *Balanteodrilus*, they are located in 18/19. The most advanced degree of transformation is thus to be found in *Torresiella*, in which the male and prostatic ducts are intimately associated (?fused) behind the combined pore. This condition is approached in *Dichogaster ehrhardti*, where, according to Michaelsen (1898): '... der Samenleiter ... in die vordere Fläche einer winzigen, atrium-artigen Hypodermis-Einsenkung ausmündend, in deren Grunde der Prostatoporus liegt'.

Why the balantine condition should be so rare is not known. In the acanthodrilid genera examined by the author, there is a distinct tendency for the anterior prostatic glands to be conspicuously larger than the posterior organs. Correspondingly, the anterior spermathecae are often smaller than those posterior. Again, there is no satisfactory explanation for these observations, but they do indicate a certain predisposition to the

microscolecine reduction. Intermediate stages in reduction suggest that in either reduction, elimination of one of the prostatic sets is a gradual process. The migration of the terminal end of the vas deferens must be largely influenced by the differential effects of the two prostatic pairs. This is presumed to be an embryonic phenomenon, the relative size of the prostatic primordia having a deterministic effect on the length of the vas deferens and the positioning of the male pore (the 'balanced' effect of subequal prostatic sets resulting in an equatorial or slightly presetal position of the male pore, as is commonly the case). A gradualist interpretation, where the male pore migrates progressively over many generations owing to some external selective force, though difficult to accept, appears to be appropriate in this instance. In cases where the male pore fails to migrate despite elimination of either prostatic pair, stabilising selection or some other influence may be involved.

#### ACKNOWLEDGMENTS

The author is indebted to Prof. B.G.M. Jamieson, University of Queensland, for considerable practical assistance and stimulating discussion in the preparation of this paper.

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# **ECHOLLOCATION AND ROOST SELECTION IN SEMON'S LEAF-NOSED BAT *HIPPOSIDEROS SEMONI***

*SEMONI*. *Memoirs of the Queensland Museum* 42(1): 158. 1997. - Seimon's Leaf-nosed Bat *Hipposideros semoni* occurs from Cape York Peninsula to Townsville, with an isolated record W of Calliope (Schulz & de Oliveira, 1995). Hall & Richards (1979) noted this bat roosting in tree hollows and deserted buildings in rainforest areas. Hall (1995) noted its roosting in caves, mines and rock overhangs and an array of artificial roost sites, including the door handle of a car, a clothes closet, an oven and a picture rail. All recorded roosts have been of individuals (Hall, 1995) except for a ♂ and ♀ together in a cave (Schulz & de Oliveira, 1995). Little is known about roost selection and no maternity sites have been located. Known roosts near Coen have been destroyed through mining (Richards & Hall, 1994). The species is known from 10 subterranean roosts and is classified nationally as rare (Hall, 1995; Richards & Hall, 1994).

We report echolocation and roost selection in a tower karst on Kings Plains Station (15°38' S, 144°58' E), SW of Cooktown, 26-28 June, 1996. The tower consisted of 2 outcrops of Ma, surrounded by semi-evergreen notophyll vine thicket up to 200m wide. Caves and fissures (32) were investigated, by a single person using a Petzl headlamp. Roosting bats were identified without being disturbed; flying bats were captured with a hand net, identified and released.

Three individuals were roosting singly in rock fissures with a southerly aspect within a radius of 30m of each other. The first was a nulliparous ♀, forearm 48.6mm and weight 9.2gm, roosting in a narrow fissure 2.1m high and 0.6m wide, 5m from the entrance. Relative humidity was 6% higher than at the entrance; temperature was the same. No other bats were roosting in this fissure. The second was a ♂ in non-breeding condition roosting 7m from the entrance in a narrow fissure 1.2m high and 0.5m wide. This fissure was deep, with two chambers at least 25m long; at the extremity of one chamber were 3 roosting Dusky Leaf-nosed bats, *Hipposideros ater*. The *H. semoni* roost site in this fissure had a relative humidity 2% lower than outside the entrance while the temperature was 3.2°C warmer. The third individual could not be caught as it was roosting in a tight fissure 0.3m wide, 5m from a near vertical entrance 3.5m by 0.4m wide. The relative humidity in this roost was 7% lower than outside the entrance.

Beneath 2 of the roosts were remains of huntsman spiders and beetle elytra suggesting they may have been prey items. The probable taking of huntsman spiders suggests that this species may be a partial 'gleaner', taking prey from surfaces such as rock faces or tree trunks. The captured ♂ and ♀ were in non-breeding condition. Other bats roosting in nearby fissures and short caves where no *H. semoni* were located were the Eastern Horseshoe bat, *Rhinolophus megaphyllus*, *H. ater* and the Common Shearwater bat, *Taphozous georgianus*.

Echolocation calls of the captured ♀ produced 284 ultrasonic sequences on 2 tapes, using the Anabat II System (Corben, 1989) and a Realistic VSC-2001 cassette recorder; 135 sequences outside the entrance of the cave (98 perching in a butterfly net, and 37 while being held), and 149 sequences after its release into the cave. Upon release, the bat hung on a rock wall and emitted ultrasonic pulses. Both recording sessions lasted 1 hour; sequences outside the cave were from 4 hours before dusk, whereas those inside were done on the hour prior to dusk. The bat was then left alone for 11 minutes, to record its emergence calls. The bat emerged at 19:07 when it was dark but moonlit, without emitting echolocation calls. Simmons & Stein (1980), characterised the echolocation calls of hipposiderid bats as having a Constant Frequency (CF) component, followed and often preceded by Frequency Modulated components (FM). Each of these sequences was examined within Anabat II and recalibrated from a recorded 40KHz

calibration tone. The CF components were also measured. Regardless of where the recordings were made, all sequences showed a CF component at 78KHz, 9KHz higher than hand-held *Rhinolophus megaphyllus* in the same outcrop (Fig. 1), which fits its frequency range recorded in SE Qld (M.C. de Oliveira, unpubl. data). The sequences of *H. semoni* from Kings Plains were 2-4KHz lower than using a QMC bat detector and different software call analysis package (Coles, 1993). The single roost of *H. semoni* was reminiscent of roost sites of the Northern Leaf-nosed bat, *H. stenotis* (Schulz & Mekhorst, 1985, 1986). *H. stenotis* specimens were also encountered as individuals roosting close to disused mineshafts in semi-dark conditions.

## **Acknowledgements**

We thank Lana Little for directions and details on the first record at Kings Plains; David Hannah for assisting in fieldwork; the manager of Kings Plains for allowing access and G. Smith for logistical support.

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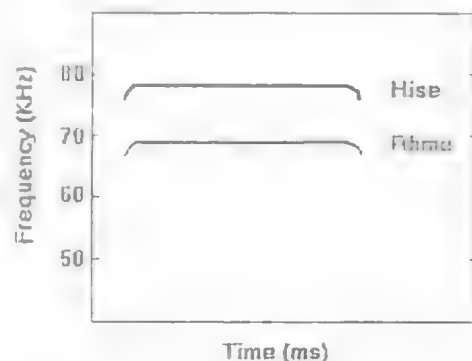


FIG. 1. Schematic representation of ultrasonic signal of *H. semoni* (Hise) and *R. megaphyllus* (Rhine), Kings Plains Sm.

# BIOMETRICS OF THE BIRDS OF PARADISE (AVES: PARADISAEIDAE): WITH OBSERVATIONS ON VARIATION AND SEXUAL DIMORPHISM

CLIFFORD B. FRITH AND DAWN W. FRITH

Frith, C.B. & Frith, D.W. 1997 06 30: Biometrics of the birds of paradise (Aves: Paradisaeidae): with observations on variation and sexual dimorphism. *Memoirs of the Queensland Museum* 42(1): 159-211. Brisbane. ISSN 0079-8835.

The Australasian bird of paradise family Paradisaeidae is presently considered to consist of 42 species. The family includes species groups and species exhibiting morphological, ecological, zoogeographical and behavioural characters of fundamental interest to many disciplines of science. Over recent years there has been an exponentially rapid increase in interest in bird of paradise biology and systematics at all taxonomic levels. Biometrical data presented here are by far the most comprehensive and directly comparative gathered for the Paradisaeidae at the family, generic, specific and subspecific levels. Mean values and ranges of measurements of each subspecies are given, and interspecific and intraspecific size variation and sexual dimorphism discussed. These data and others are used to assess the validity of bird of paradise subspecies discussed by recent authors. □ *Paradisaeidae, Birds of Paradise, systematics, sexual dimorphism, morphometrics.*

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The Australasian bird of paradise family Paradisaeidae is presently considered to consist of 42 species constituting 16 genera and involving a total of approximately 100 subspecies (Gilliard, 1969), to which a few have been added more recently. Birds of paradise include species groups and species exhibiting morphological, ecological, zoogeographical and behavioural characters of fundamental interest to many disciplines of science (Diamond, 1981, 1986; Beehler, 1989; Johnsgard, 1994). Thus there is a large literature about birds of paradise including at least nine major monographs, in addition to more general works and hundreds of scientific publications (Frith, 1979). Moreover, over recent years there has been an exponentially rapid increase in interest in their biology and systematics at all taxonomic levels (Bock, 1963; Gilliard, 1969; Diamond, 1972, 1986; Pruett-Jones & Pruett-Jones, 1988, 1990; Beehler, 1989; Sibley & Ahlquist, 1990; Clench, 1985, 1992; Cracraft, 1992; Christidis & Schodde, 1991, 1992; Frith, 1992; Frith & Cooper, 1996; Frith & Frith, 1990, 1992, 1993a,b, 1994, 1995, 1996a,b, in press).

Birds of paradise attract considerable attention because of the elaborate to bizarre plumage of adult males that are related to the polygynous mating system of most sexually dimorphic (and some sexually monomorphic) species and promiscuity in males. For details of their general appearance and biology see Gilliard (1969), Cooper & Forshaw (1977), Beehler et al. (1986) and Coates (1990). Promiscuous adult male birds of

paradise show remarkable interspecific diversity of highly colourful and ornate plumages, which they use in highly ritualized and complex solitary or communal (lek or exploded lek) courtship displays at traditional sites, perches or courts (Diamond, 1986; Beehler, 1989). A remarkable feature of these birds, and stressing the close genetic relationships between them, is the marked diversity of intra- and inter-generic hybrids (Stresemann, 1923, 1930, 1934; Mayr, 1941; Gilliard, 1969; Fuller, 1979, 1995). The vast majority of known hybrid specimens are in full or subadult male plumage (Fuller, 1979), but recently two hybrids have been described in female plumage (Frith & Frith, 1996a, b). One of the latter, a unique hybrid between *Lophorina superba* and *Parotia carolae*, was until recently erroneously known as *Lophorina superba pseudoparotia*.

Birds of paradise are so conspicuously significant to sexual selection theory that they were described and discussed at length by Wallace (1869) and Darwin (1871), and innumerable authors since (see references in Frith, 1979; Diamond, 1981; Beehler, 1989; Johnsgard, 1994). In attempting to understand the evolutionary origins and functions of polygynous mating systems and the role and influence of sexual selection within them, it is important to know the physical attributes of the species concerned. In particular one must be aware of fundamental sexual dimorphism (in characters other than secondary sexual ones such as adult male plumage). Sexual dimor-



phism in size is particularly significant as it is usually conspicuous in polygynous vertebrates in which males are typically larger than females, but is reversed in polyandrous species in which females may be larger than their multiple mates (Darwin 1871). Notwithstanding the enormous literature on the birds of paradise, no study has been devoted to comprehensively demonstrating and reviewing variation in size between the species, sexes and their subspecies. No publication presents more than the vaguest of measurements for only the smallest of samples. Most of them in fact fail to indicate any sample sizes.

The monograph by Gilliard (1969) is the standard modern text for comparative bird of paradise measurements at the species level, but only size ranges for some basic characters are provided therein. No sample sizes are given and few, if any, are presented for the vast majority of subspecies. Cooper & Forshaw (1977) presented measurements for 'five or more specimens' of nominate subspecies of each species only. The only subgroups for which reasonable data have been presented in recent years are those of the Glossy-mantled Manucode *Manucodia ater* (Gilliard, 1956) and of all *Paradisaea* species (LeCroy, 1981). As the latter two studies were based predominantly upon specimens in the American Museum of Natural History, they understandably present relatively small sample sizes compared to those presented here.

Several authors have discussed the validity of various bird of paradise subspecies with respect to plumage morphology and relative sizes (Gilliard, 1969; Schodde & McKean, 1972, 1973; Diamond, 1972; Coates, 1990; Cracraft, 1992). Cracraft dramatically revised the systematics of the family by applying the 'phylogenetic species concept' (Cracraft, 1992 and references therein). This in large part involved Cracraft reviewing the subspecies acknowledged by Gilliard (1969) and elevating the vast majority of them to 'species' level. Cracraft (1992) considered 25 of the bird of paradise subspecies recognised by Gilliard (1969) to be not 'diagnosably distinct', and therefore reduced them to synonymy in accord with his phylogenetic species concept. He recognised one 'species' named since Gilliard's monograph (*Epimachus fastuosus ultimus*, Diamond, 1969) and named two new 'species' himself (*Manucodia [keraudrenii] aruensis* and *M. [keraudrenii] diamondi*).

All of the above authors expressed the view that a number of subspecies (valid or invalid 'species' of Cracraft, 1992) were possibly or probably in-

valid but that more comparative material, or other types of evidence, were required for firm conclusions. While larger series of skins of some taxa were available to us in a single collection, or were gathered together at a single institution, for comparative review of plumage morphology this was not possible for the majority of the subspecies. Thus, we seek here to primarily use the considerable biometrical data we accumulated to assess the validity of bird of paradise subspecies presented by Gilliard (1969), Diamond (1972) and subsequent authors (Cracraft, 1992; and references therein). The value of observed differences in average size between populations has limitations given that size is a continuously varying character. It is more useful to plot individual specimens over the geographical range of a taxon in order to perceive any clinal variation in size, but this approach is most rarely applied and is well beyond the scope of the present study. It is clear, however, that biometric data available prior to this study are grossly inadequate and have led to numerous erroneous statements concerning the sizes of some characters of some taxa and others concerning supposed sexual dimorphism in size (see below).

The present re-evaluation of bird of paradise taxa in the light of significant biometrical data sets is timely both in terms of complimenting and assessing Cracraft's (1992) revision of plumage morphology. Moreover, it provides basic evidence supporting the subspecific taxonomy to be followed in a forthcoming monograph of the biology of the group (Frith & Beehler, in prep.). This is desirable as it will not be possible to present and discuss the significant supporting biometrical data in that forthcoming work. Accepted genera and their sequence are those of Beehler & Finch (1985), with the addition of those taxa extralimital to New Guinea and therefore not dealt with in that publication. As taxa accepted by Gilliard (1969) form the basis for contemporary studies, we follow here his systematics and scientific names at the species and subspecies level (more recently described taxa accepted). The latter are presented in chronological order of description.

Data sets herein provide a significant resource to students of the systematics and biology of the group and also to those interested in sexual selection and size dimorphism in an avian group (including both polygynous and monogamous mating systems) or avian biometrics in general. Beyond that, a data set of this magnitude for an entire avian family will prove of value to biology

students with an interest in more general studies of systematics, speciation, sexual and other dimorphism.

## METHODS

During a recent world tour of larger collections of bird of paradise skins the authors examined all sexed specimens from a recorded locality. Museum specimens were examined at or from (on loan to us) the following institutions: Queensland Museum, Brisbane; Australian National Wildlife Collection, CSIRO, Canberra; Australian Museum, Sydney; Museum of Victoria, Melbourne; South Australian Museum, Adelaide; Western Australian Museum, Perth; American Museum of Natural History, New York; The Natural History Museum, London; Museum of Vertebrate Zoology, University of California, Berkeley; The Field Museum, Chicago; Museum of Comparative Zoology, Cambridge; Bernice Pauahi Bishop Museum, Honolulu; Royal Ontario Museum, Toronto; Academy of Natural Sciences, Philadelphia; The Carnegie Museum of Natural History, Pittsburgh; Peabody Museum, Yale University, New Haven; Delaware Museum of Natural History, Wilmington; National Museums & Galleries, Liverpool; Nationaal Natuurhistorisch Museum, Leiden; Swedish Museum of Natural History, Stockholm; Zoologisk Museum Københavns Universitet, København; Museum national D'Histoire Naturelle, Paris; Staatliches Museum für Tierkunde, Dresden; Zoologische Staatssammlung, München; Zoologische Museum Berlin; Museum Alexander Koenig, Staatliches Museum für Naturkunde, Stuttgart; Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt; Zoologisches Institut und Zoologisches Museum, Hamburg; Museum Zoologicum Bogoriense, Bogor; National Museum and Art Gallery of Papua New Guinea, Port Moresby.

A sample of at least 25 individuals for each sex and age class for each subspecies accepted by Gilliard (1969) was measured where possible. Measurements were all taken in the same standard way with the same instruments by CBF. 'Wing length' is the flattened and straightened chord and was measured with a stopped steel decimal rule. 'Tail centrals' is the maximum length of the longest of the central pair of rectrices from the point of feather entry into the skin to its tip, and 'tail length' the same but to the tip of the longest tail feather other than the central pair. Tail measurements were made with an unstopped

small steel decimal rule. When the central and outer tail rectrices are the same length, or nearly so (<3mm difference), only the longer measurement (usually tail length) is presented as 'tail length', unless there is intrageneric variation, and then both 'tail centrals' and 'tail length' are given.

Other measurements were taken with steel electronic digital vernier calipers to the nearest whole decimal point and checked and zeroed daily. 'Bill length' is from the union of the bill with the fore skull to the tip of the upper mandible, and 'bill width' from the anterior nostril edge. 'Total head length' is the maximum distance from the back of the skull to the tip of the upper mandible. It was measured only from specimens retaining sufficient of the rear skull to permit it. It is possible some specimens that appeared complete in this respect may not in fact have been so and therefore the total head length figures presented must be considered minimum ones. 'Tarsal length' is from the intertarsal joint to the lower edge of the last undivided scute (scale) before the toes diverge. Where possible, all of these measurements were taken from a total of 5677 museum specimens. Weights, recorded upon death of the bird, were noted from the labels of measured specimens and also from those of an additional 408 skins that we did not measure (total specimens being 6085). We also include additional weights ( $n = 298$ ) obtained from living birds by ourselves or others trapping and releasing them.

In certain bird of paradise groups species have peculiar or unique feathers that provided additional measurements useful for an examination of possible intraspecific variation. In *Manucodia keraudrenii* we measured the length of 'ear tufts' of feathers from their posterior base to the tip of the longest with a small unstopped steel rule. Likewise we measured the structurally similar tuft of feathers at the base of the 'flag'-tipped occipital plumes in adult male *Parotia* species and the analagous single elongate 'ear' feather found in female-plumaged *Pteridophora alberti*. The maximum length of the longest occipital plumes of both *Parotia* species and *Pt. alberti* and the crest length of *Cnemophilus macgregorii* were likewise measured. The maximum length of the modified upper wing coverts or 'standants' of *Semioptera wallacei* are also presented. The length of pectoral flank plumes (of *Seleucidis paradisiae*, etc.) are rather more subjective and give only an indication of relative flank plume size. This involved laying the male specimen on its back with the end of a steel rule at the tip of the tail and subjectively assessing the average length of

the bulk of plumes (excluding odd finer and longer feather tips) projecting beyond the tail tip.

In Tables 1-42 we present mean values, standard deviations, ranges and sample sizes for each measured character of each sex and age class of all subspecies, and for each species as a whole. Data for markedly sexual dimorphic species in which males may have an adult, subadult (trace to almost complete adult male plumage intruding into female plumage) and immature male (female-type) plumage are presented separately for each male age group. Data for females of those species whose plumage is generally similar at all ages, are presented collectively. The latter are referred to as adult females despite the fact that samples will inevitably include some individuals less than adult given the great similarity in plumage, but data for individuals smaller than adult size (i.e., juveniles to immatures) are excluded. Data for basically monomorphic species, in which adult males and adult females are generally similar but have a discernibly different immature plumage, are given separately for each immature sex. A single exception is *Loboparadisea sericea* for which we combine data for immatures and subadults of both sexes as the very few specimens of birds in the latter plumage did not warrant their separation.

In the species accounts we cite the original description and type locality of each taxon after the species name, if monotypic, or after each subspecies name. Early synonyms are not presented. We discuss the biometric data for the species as a whole, and for subspecies where it is necessary to point out differences in size and proportions between them. We do not here fully describe plumages of nominates or describe and discuss distributions of the various taxa unless pertinent as these are widely available (Gilliard, 1969; Cooper & Forshaw, 1977; Cracraft, 1992) and will be presented anew in a forthcoming monograph (Frith & Beehler, in prep.).

Because bird of paradise measurements presented in Gilliard (1969) and Cooper & Forshaw (1977) are those referred to in the contemporary ornithological literature we make specific observations upon them as and when required. Our relatively large sample sizes enable us to critically evaluate previously published assessments of several size-related characters and have in some cases found them misleading or erroneous. Gilliard (1969) and Cooper & Forshaw (1977) present 'culmen length' as opposed to bill length. Culmen length is that of the exposed culmen and is taken from the point where forehead feathers

no longer cover the culmen to the bill tip. This is not a measurement of a discrete structure and is far more subjective (and variable) than 'bill length' (from anterior margin of the skull to the bill tip). Thus the culmen measurements of Gilliard (1969) and Cooper & Forshaw (1977) are consistently shorter than ours and we will not allude to them again unless to note their inherently misleading nature (see *Lophorina superba* below).

The following abbreviations are used below: A = adult; SA = subadult; I = immature; MWL = mean wing length; MTL = mean tail length; MTCL = mean tail central length; MLL = mean tarsal length; THL = total head length; MBL = mean bill length; MBW = mean bill width; MW = mean weight; METL = mean ear tuft length; MOPL = mean occipital plume length; MFPL = mean flank plume length.

## RESULTS AND DISCUSSION

### PARADISAEIDAE CNEMOPHILINAE

#### *Cnemophilus macgregorii* Crested Bird of Paradise (Table 1).

A ♀ similarly sized to or slightly smaller than A ♂, and of similar proportions, MWL and MW by 4 & 7% respectively. MTL similar in A ♀, A ♂ and I ♂. Thus, ♂ do not acquire a progressively shorter tail with age (as in *C. loriae*). MTL as a proportion of MWL similar in both sexes, 80 & 82% respectively. MLL and MBL of A ♀ 3 & 9% shorter than in A ♂ respectively, but similar in proportion to MWL in both sexes. Crest lengths of A ♂ and SA ♂ average  $34 \pm 4$  mm ( $n = 51$ ) &  $32 \pm 3$  mm ( $n = 9$ ) respectively, but shorter in I ♂, and A ♀, averaging  $19 \pm 6$  mm ( $n = 22$ ) &  $17 \pm 4$  mm ( $n = 25$ ) respectively.

1) *C. m. macgregorii* De Vis, 1890. Annual Report of British New Guinea 1888-89: 62. Mt Knutsford (erroneously Mt Musgrave in Gilliard 1969), Owen Stanley Mts. Wing lengths of 116-121 mm for A ♂ and 115-120 mm for A ♀ presented by Cooper & Forshaw (1977) are inexplicably long given that our measurements are of maximised wing lengths.

2) *C. m. sanguineus* Iredale, 1948. Australian Zoologist 11: 162. Kumdi, Mt Hagen District. Like nominate but generally more red, being orange-red about head, less red on back to orange rump, underparts with less copper-red suffusion. MWL slightly larger, but MTL slightly shorter, than nominate.

3) *C. m. kuboriensis* Mayr & Gilliard, 1954. Bulletin of the American Museum of Natural History 103: 361. Mt Orata, Kubor Mts. Upperparts of A ♂ very like *sanguineus* but slightly paler, less saturated with red and underparts more black, less suffused with red-brown. Characters supposedly distinguishing this subspecies from *sanguineus* have been doubted (Diamond, 1972; Beehler in Coates, 1990; Cracraft, 1992); we found a Mt Giluwe specimen of *C. m. sanguineus* showing these characters. MWL and MTL of *kuborensis* slightly shorter than *sanguineus*, but samples too small for meaningful comparisons. Morphology does suggest, however, that *kuborensis* is invalid and should be synonymised with *sanguineus*.

4) *C. m.* subspecies. Gilliard (1969) was brought an A ♂ specimen in the field said to come from the Kraetke Mts, where the species is unrecorded, which was paler than Wahgi Highlands birds. He felt that if the specimen was not faded it might represent an unknown subspecies. An A ♂ specimen in Zoologische Museum, Hamburg from Malingdam, near Mt Goliath, Irian Jaya, we examined also fits this description but could possibly be the result of immersion in alcohol. Its wing, tail, tarsal and bill lengths measure 115, 86, 43.6 & 29.4mm respectively; bill width 6.3mm and weight 90g. These measurements are within the ranges of other subspecies.

#### *Cnemophilus loriae* Loria's Bird of Paradise (Table 2)

A ♀ similar to or only fractionally smaller than A ♂, and of similar proportions, MWL similar but MW 5% lighter. MTL of A ♀ and I ♂ slightly longer (3 & 5% respectively) than A ♂. Thus, ♂ acquire a progressively shorter tail with age. MTL 71 and 74% of MWL in A ♂ and A ♀ respectively, so proportionately longer in A ♀. MLL and MBL of A ♀ negligibly (2%) shorter than in A ♂, but similar in proportion to MWL in both sexes.

1) *Cnemophilus l. loriae* Salvadori, 1894. Annals Museo Civico Genova, ser 2, 14: 151. Moroka, Owen Stanley Mts. Iridescence on tertials of A ♂ blue.

2) *Cnemophilus l. amethystina* Stresemann, 1934. Ornithologische Monatsberichte 42: 144. Schraderberg, Sepik Mts. Iridescent upper surfaces of tertials of A ♂ deep violet-purple, but A ♀ as other subspecies. Similar in size to nominate, but MWL and MTL slightly longer than in other subspecies.

3) *Cnemophilus l. inexpectata* Junge, 1939. Nova Guinea, new series 3: 77. Bijenkorf, Oranje Mts. Iridescence of tertials of A ♂ more green than the blue of *loriae* or the violet-purple of *amethystina* but A ♀ as other subspecies. Similar in size to nominate, with MTL only slightly shorter than nominate and (more so) *amethystina*.

#### *Loboparadisea sericea* Yellow-breasted Bird of Paradise (Table 3)

A ♀ (uniquely in the Paradisaeidae) slightly larger than, but similarly proportioned to, A ♂, MWL and MW (sample small) by 2 & 14% respectively. MTL of A ♀ and I ♂ slightly longer (4 & 7% respectively) than A ♂. Thus, ♂ acquire a progressively slightly shorter tail with age. MTL 59 & 61% of MWL in A ♂ and A ♀ respectively. MLL similar in length and in proportion to MWL in both sexes, MBL of A ♀ 5% longer than in A ♂, but similar in proportion to MWL in both sexes.

1) *L. s. sericea* Rothschild, 1896. Bulletin of the British Ornithologists' Club 6: 16. 'Dutch New Guinea'. Restricted to the Weyland Mts (Mayr, 1941). ♀ said to be larger than ♂ (age unspecified) in the Weyland Mts but not so on Mt Karimui (Diamond, 1972). Certainly ♀ from the Weyland Mts have longer wings and tails than those on Mt Karimui but Diamond's samples are too small (A ♂ x 1; I ♂ x 1, ♀ x 2) for meaningful comparisons.

2) *L. s. aurora* Mayr, 1930. Ornithologische Monatsberichte 38: 147. Dawong, Herzog Mts. Plumage of upperparts significantly brighter (paler), more brown-yellow, the crown far paler and more greenish and less brown, but underparts similar to *sericea*. Larger than nominate, MWL and MTL of A ♂ by 3 & 7% respectively. While not discussing it, Cracraft (1992) appeared to reject Diamond's (1972) attribution of birds from the Mt Karimui area, Papua New Guinea to the nominate (where we have also included them) and considered them to be *L. s. aurora*. If, however, they are *aurora*, their measurements would be at the lower end of the size range for this subspecies.

#### PARADISAEINAE

##### *Macgregoria pulchra* Macgregor's Bird of Paradise (Table 4)

A ♀ markedly smaller than, but similarly proportioned to, A ♂, MWL, MTL and MW (sample small) by 11, 11 & 26% respectively. I ♂ and SA ♂

have not been collected or are difficult to differentiate and so it is unknown if MTL increases or decreases with age. MTL 76% of MWL in both sexes. MLL and MBL of A ♀ 8 & 6% shorter than in A ♂ respectively, but similar in proportion to MWL in both sexes.

This sexual size dimorphism is distinctly different from all three members of the subfamily Cnemophilinae and is greater than the majority of polygynous Paradisaeinae. Its extent is unusual in a monogamous bird of paradise (Rand, 1940; Beehler in Coates 1990).

1) *M. p. pulchra* De Vis, 1897. Ibis 1897: 251, pl. 7. Mt Scratchley, south-eastern New Guinea. Wing lengths of 188–193 mm for A ♀ (Cooper & Forshaw, 1977) are inexplicably large given our measurements are maximised wing lengths.

2) *M. p. carolinae* Junge, 1939. Nova Guinea (New Series) 3: 82. Oranje Mts. Proportionally different from nominate, MWL and MTL shorter by 5 & 6% and 17 & 16% and MLL longer by 5 & 4% in A ♂ and A ♀ respectively. Weights of *carolinae* heavier than *pulchra*, but samples too small for meaningful comparisons.

#### ***Lycocorax pyrrhopterus* Paradise Crow** (Table 5)

A ♀ similar to or slightly smaller than A ♂ in size, proportions and notably weight, MWL, MTL and MW by 3, 4 & 12% respectively. I ♂ have not been collected or are difficult to differentiate and so it is unknown if MTL increases or decreases with age. MTL 73% of MWL in both sexes. MLL and MBL of A ♀ 2 & 5% shorter than in A ♂ respectively, but similar in proportion to MWL in both sexes.

1) *L. p. pyrrhopterus* (Bonaparte, 1851). Conspectus Generum Avium 1 (1850): 384. Gilolo I. Concealed bases of primaries with no white. MTL 75% of MWL in both sexes.

2) *L. p. morotensis* Schlegel, 1863. Ibis 1863: 119. 'Mortag'. Much like nominate but paler, slightly more brownish above but slightly darker below. Concealed bases of primaries extensively white. Significantly larger than the other two subspecies in all measured characters. MTL 71 & 69% of MWL in A ♂ and A ♀ respectively, and thus similar to *obiensis* but proportionally shorter than nominate. MWL and MTL of A ♂ 15 & 9% and 7 & 8% longer than in A ♂ *pyrrhopterus* and *obiensis* respectively; these figures slightly less (12 & 4%, 6 & 3%) for A ♀.

3) *L. p. obiensis* Bernstein, 1864. Journal für Ornithologie 12: 410. Obi Is. Generally like nom-

inate but distinct in being much darker overall, much more glossy blue-green, darker and more blue-black on crown and uppertail. Far more different from nominate than *morotensis* and possibly approaching species status (Cracraft, 1992). Concealed bases of primaries with trace of white only. Oddly Lambert (1994) incorrectly wrote of *obiensis* that birds have a whitish streak above and behind the eye. Larger than nominate in all measured characters. MTL 71% of MWL in both sexes and thus proportionately shorter than nominate.

#### ***Manucodia atra* Glossy-mantled Manucode** (Table 6)

A ♀ similar to or slightly smaller than A ♂ in size, proportions and notably weight, MWL, MTL and MW by 4, 6 & 13% respectively. I ♂ and I ♀ smaller than respective adults in MWL (6%) & MTL (7 & 5%), and lighter (sample small). Thus, tail length increases with age in both sexes. MTL 84 & 83% of MWL in A ♂ and A ♀ respectively. The tail/wing index for both sexes combined ranges from 84–89%, these figures similar to those given (82–88%) by Coates (1990). MTL longer than other *Manucodia* species, excluding *M. comrii*. MLL and MBL of A ♀ 3 & 5% shorter than in A ♂ respectively, but similar in proportion to MWL in both sexes.

Since a thorough study by Gilliard (1956), resulting in the acceptance of the three subspecies, only Cracraft (1992) has reviewed the species. In assessing plumage variation, from the phylogenetic species concept point of view, Cracraft considered there to be no diagnostic characters within *M. atra* populations. We agree with Gilliard, however, that it would be misleading to include all populations in a single taxon in the face of what in fact are quite gross plumage differences apparent at the extremes of the range of this species and the clear differences in size demonstrated here. We therefore follow Gilliard's treatment until genetic studies provide definitive answers to this complex problem. Our measurements of wing and tail for the species as a whole agree closely with those of Gilliard (1956); but his exposed culmen is not comparable with our bill length and his tarsal length range is larger than ours, indicating differing measuring techniques.

1) *M. a. atra* (Lesson, 1830). Voyage of the Coquille, Zoology 1: 638. Dorey, north-western New Guinea.



2) *M. a. alter* Rothschild & Hartert, 1903. *Novitates Zoologicae* 10: 84. Sudest I. Flanks and belly markedly more violet than *atra*. Notably larger than nominate, A♂ by 12 & 15% and A♀ 9 & 12% in MWL and MTL respectively. MLL, THL and MBL of A♂ exclusively larger than nominate and nearly so in A♀.

3) *M. a. subalter* Rothschild & Hartert, 1929. *Bulletin of the British Ornithologists' Club* 49: 110. Dobbo, Aru Is. Said to average much more purple and violet with oil-green rare on adults (Gilliard, 1969). On average larger than nominate, but smaller than *alter*. An analysis more thorough than is possible here is required in order to test the possibility that birds are clinal in size from larger ones in the extreme south-east of Papua New Guinea to smaller ones toward the extreme southeastern-most part of the range of the generally smaller nominate on the Gulf of Papua.

***Manucodia chalybata* Crinkle-collared  
Manucode (Table 7)**

*M. chalybata* (Pennant, 1781). *Specimen Faunula Indica*, in Forster's *Indian Zoology* 1781: 40 (based on Daubenton, *Planches Enluminées*, pl. 634). New Guinea, restricted to the Arfak Mts. Monotypic. A♀ similar to or slightly smaller than A♂ in size, proportions and weight, MWL, MTL and MW by 3, 4 & 3% respectively. I♂ and I♀ smaller than respective adults in MWL (2 & 4%) and MTL (6 & 4%), and lighter (sample small). Thus, tail length increases with age in both sexes. MTL 82 & 81% of MWL in A♂ and A♀ respectively. The adult tail/wing index for both sexes combined ranges from 81-84%, these figures within the range of those (78-86%) presented by Coates (1990). MLL and MBL of A♀ 2 & 5% shorter than in A♂ respectively, but similar in proportion to MWL in both sexes.

The tarsal lengths of 41-45mm for A♂ and of 39-46mm for A♀ of Cooper & Forshaw (1977) do not agree with our measurements. This species is difficult to differentiate from *M. jobiensis* in almost all external morphology as they are generally similar and overlap in most measurements, but the latter species does have a (5-6%) shorter tail proportionate to wing length.

***Manucodia comrii* Curl-crested Manucode  
(Table 8)**

A♀ slightly smaller than A♂ and of similar proportions, MWL and MTL by 5 & 4% respectively. I♂ and I♀ smaller than respective adults,

but samples too small for meaningful comparisons, MTL 71% of MWL in both A♂ and A♀. The adult tail/wing index for both sexes combined ranges from 70-76%, MLL and MBL of A♀ 3 & 6% shorter than in A♂ respectively, but similar in proportion to MWL in both sexes.

Gilliard's (1969) A♂ tarsal length of 57 mm and Cooper & Forshaw's (1977) of 54-59 mm for both sexes are very long.

1) *M. c. comrii* Selater, P.L. 1876. *Proceedings of the Zoological Society of London* 1876: 459. Hoon Gulf in error for Ferguson I.

2) *M. c. trobriandi* Mayr, 1936. *American Museum Novitates* 869: 3. Kaileuna, Trobriand I. Plumage as nominate with MWL and MTL shorter by 7 & 9% and 6 & 7% in A♂ and A♀ respectively. Thus, this subspecies is on average smaller than the nominate with limited overlap in size ranges of wing and tail in each adult sex. Taking this and the two island populations' allopatry into account it seems on balance more useful to recognise their differences than to conceal them, notwithstanding their possibly questionable status (Cracraft, 1992).

***Manucodia jobiensis* Jobi Manucode  
(Table 9)**

A♀ similar to or slightly smaller than A♂ in size, proportions and notably weight, MWL, MTL and MW by 4, 5 & 21% respectively. I♂ and I♀ smaller than respective adults in MWL (3 & 2%) and MTL (4 & 6%), but samples small. Thus, tail length increases with age in both sexes. MTL 76 & 75% of MWL in A♂ and A♀ respectively. The adult tail/wing index for both sexes combined ranges from 72-76%, these figures within the range of those (69-78%) presented by Coates (1990). MLL and MBL of A♀ 3 & 5% shorter than in A♂ respectively, but similar in proportion to MWL in both sexes.

We can generally reconcile our measurements with those for the species by Gilliard (1969), but not at all with Cooper & Forshaw's (1977) sizes of 168-173mm for wing and 42-44mm for tarsus for A♂ and 165-172mm for wing and 40-45mm for tarsus for A♀ of nominate, which are exclusively too small (wing) or too large (tarsus).

1) *M. j. jobiensis* Salvadori, 1876. *Annali Museo Civico Genova* 7 (1875): 969. Wonapi, Jobi (= Yapen) I. Only known from Yapen I in Geelvink Bay, west Irian Jaya.

2) *M. j. rubiensis* Meyer, 1885. *Zeitschrift für die gesammte Ornithologie* 2: 374. Rubi, Geelvink Bay. Now known from the mainland coast

of northern New Guinea adjacent to Yapen I eastward to the Astrolabe Bay area of Papua New Guinea and south in the west to the upper Setekwa R. and in the east the upper Ramu R. MWL and MTL shorter than nominate, by 5 & 6% and 3 & 2% in A ♂ and A ♀ respectively. Thus, the mainland birds are on average smaller than those on Yapen I (Gilliard, 1969). As samples of the latter are small ( $n = 6$ ), and wing and tail lengths ranges of mainland birds in fact entirely overlap those of the nominate island form, the validity of this subspecies remains in doubt. Gilliard (1969) described *rubensis* as similar to *jobiensis* (♂ wing length of latter 177-179mm, tail 132-142mm), but smaller (♂ *rubensis* wing length 168-174mm, tail 127-133mm). Present data are inadequate to justify the retention of *rubensis* and on the basis of this we agree with Cracraft (1992) that it should be synonymised with *jobiensis*, but more data are clearly required.

***Manucodia keraudrenii* Trumpet Manucode**  
(Table 10)

A ♀ similar to or slightly smaller than A ♂ in size, proportions and notably weight, MWL, MTL and MW by 4, 5 & 12% respectively. I ♂ and I ♀ smaller in MWL (5 & 3%) and lighter (sample small) than respective adults, but only I ♂ MTL negligibly shorter (2%). Thus, tail length increases only slightly with age in ♂, those of I ♀ and A ♀ being similar. MTL 78% of MWL in both sexes. The adult tail/wing index for both sexes combined ranges from 73-78%, these figures being within the range of those (70-81%) presented by Coates (1990). MLL and MBL of A ♀ 3 & 5% shorter than in A ♂ respectively, but similar in proportion to MWL in both sexes. Proportionate bill length is remarkably consistent, MBL 21% of MWL in all subspecies except *hainsteini* and *gouldi* for which it is 20%.

A difficult species complex within which Gilliard (1969) acknowledged eight subspecies, which Cracraft (1992) reduced to seven ('species') by synonymising *M. k. mayeri* with *M. k. purpureoviolaceus*. To these, Cracraft (1992) added two newly described forms. Cracraft's (1992) efforts notwithstanding, more collecting and study of this species are required to meaningfully understand distributions and intraspecific variation given the patchiness of collecting on mainland New Guinea and the subjective nature of plumage characters used (colour and quality of refracted light in the form of iridescence). The length of the laceolate 'ear tufts' are also used in

subspecific diagnosis (Gilliard, 1969; Cracraft, 1992). Data for 10 subspecies are presented, eight as acknowledged by Gilliard (1969) and the two described by Cracraft (1992).

1) *M. k. keraudrenii* (Lesson & Garnot), 1826. Bulletin Scientifiques Naturelles (Ferussac) 8: 110. Dorey, Vogelkop, north-western New Guinea. METL  $19 \pm 4$ mm ( $n = 24$ ) &  $18 \pm 2$ mm ( $n = 15$ ) in A ♂ and A ♀ respectively. MTL 78% of MWL in adults.

2) *M. k. gouldi* (Grey), 1859. Proceedings of the Zoological Society of London note, p. 158. Cape York. Like nominate but plumage iridescence more green, less purple (particularly so on the upperwing and tail). Ear tuft feathering more narrowly pointed, METL  $34 \pm 6$ mm ( $n = 33$ ) &  $29 \pm 4$ mm ( $n = 16$ ) in A ♂ and A ♀ respectively. This is much longer than in *keraudrenii*, but not longer than in *purpureoviolaceus* (pace Cracraft, 1992). MTL proportionately long, 81% of MWL in adults.

3) *M. k. jamesi* (Sharpe), 1877. Catalogue of Birds in the British Museum 3: 181, Aleya, Hall Sound, British New Guinea. Throat and breast dark metallic blue, washed with green, lacking purple of nominate. Ear tufts longer than in nominate, METL  $27 \pm 5$ mm ( $n = 25$ ) &  $24 \pm 7$ mm ( $n = 25$ ) in A ♂ and A ♀ respectively. MTL 78% of MWL in adults.

4) *M. k. hainsteini* (Sharpe), 1882. Journal of the Linnean Society of London 16: 442. East Cape, New Guinea in error for Normanby I. Back, rump and uppertail are dark bluish-purple (less green) and the ear tuft feathers are less blue and more green than nominate. Generally like nominate, but much larger overall, MWL and MTL by 18 & 12% and 20 & 15% in A ♂ and A ♀ respectively. Ear tufts also longer, METL  $26 \pm 3$ mm ( $n = 11$ ) &  $22 \pm 3$ mm ( $n = 8$ ) in A ♂ and A ♀ respectively. MTL 74% of MWL in adults, so proportionately the shortest of all subspecies.

5) *M. k. purpureoviolaceus* (Meyer, 1885). Zeitschrift für die gesamte Ornithologie 2: 375, pl. 15. Astrolabe Mts. Generally like nominate but larger with back, breast and belly intensely iridescent violet-purplish. Ear tufts notably long, METL  $38 \pm 6$ mm ( $n = 35$ ) &  $34 \pm 4$ mm ( $n = 29$ ) in A ♂ and A ♀ respectively. MTL 76% of MWL in adults.

6) *M. k. neumanni* (Reichenow, 1918). Journal für Ornithologie 66: 438. Lordberg. Like similar-sized nominate but lower back, rump, uppertail and wings dark black-bluish washed iridescent deep violet-purple, not more greenish. Breast and belly dark metallic blue. METL  $13 \pm 1$ mm ( $n =$



9) &  $11 \pm 1\text{mm}$  ( $n=8$ ) in A♂ and A♀ respectively and similar to those of an otherwise overall larger *adelberti*. MTL 80% of MWL in adults.

7) *M. k. mayri* (Greenway, 1942). Proceedings of the New England Zoological Club 19: 51. Wau, Morobe District, north-eastern New Guinea. Near-identical in size/plumage to *purpureoviolaceus* and ear tufts also notably long. METL  $38 \pm 11\text{mm}$  ( $n=7$ ) &  $37 \pm 6\text{mm}$  ( $n=4$ ) in A♂ and A♀ respectively. MTL 78% of MWL in adults. The supposed evidence of a higher wing-tail index in *mayri* than in *purpureoviolaceus* (Gilliard, 1969) is meagre given limited numbers of specimens of the former. As no other characters including ear tuft length appear to differentiate them, we concur with Cracraft (1992) that *mayri* should be synonymised with *purpureoviolaceus*.

8) *M. k. adelberti* (Gilliard & LeCroy, 1967). Bulletin of the American Museum Natural History 138: 72. Nawawu, Adelbert Mts. Generally similar to nominate but like *M. k. neumanni*, with upper wings and tail more green (not, or far less, blue to purple). Ear tufts shorter than other forms except *neumanni*, METL  $13 \pm 2\text{mm}$  ( $n=10$ ) &  $14\text{mm}$  ( $n=1$ ) long in A♂ and A♀ respectively. MTL 80% of MWL in adults.

9) *M. k. aruensis* (Cracraft, 1992). Cladistics 8: 10. Wanem Bay, Kobror I, Aru I, West Irian. Much less green than nominate and differ from adjacent mainland New Guinea *jamesii* by being generally much darker and bluer, less green. Upperparts, particularly back, suffused purple, and lanceolate head feathering deeper, more purple, cobalt blue than in *jamesii*. A♂ slightly larger than nominate in MWL (5%) and more so in MTL (10%). Ear tuft length most similar to nominate, METL  $22 \pm 4\text{mm}$  ( $n=4$ ) in A♂ and thus much shorter than *jamesii*. MTL proportionately the longest, 82% of MWL in adults.

10) *M. k. diamondi* (Cracraft, 1992). Cladistics 8: 12. Awande, near Okapa, Eastern Highlands District, Papua New Guinea. Similar to *purpureoviolaceus* but defined as distinct from it in having back, upperwings and tail with strong violet-purple sheens, the breast and belly dark metallic blue with little or no violet-purple, and lanceolate head feathering bluish-green as opposed to greenish-blue washed violet-purple. Ear tufts slightly longer than in *purpureoviolaceus*, METL  $40 \pm 9\text{mm}$  ( $n=11$ ) &  $34 \pm 1\text{mm}$  ( $n=4$ ) in A♂ and A♀ respectively, and longer than in other subspecies. MTL 76% of MWL in adults.

#### *Paradigalla carunculata* Long-tailed *Paradigalla* (Table 11)

A♀ markedly smaller than A♂ in most measurements, MWL and MTL by 11 & 5% respectively. Tails of I♂ similar in length to A♀. MTL shorter than MTCL in A♀ (5%), I♂ (7%) and A♂ (18%). Thus, ♂ acquire a progressively longer tail with age, the central pair increasing considerably in length (20%) and at a far greater rate than the remainder. MTL 71 & 76% of MWL in A♂ and A♀ respectively (contra *P. brevicauda*), so proportionately longer in the ♀. MLL and MBL of A♀ 7 & 2% shorter than in A♂ respectively, but as a proportion of MWL negligibly (2 & 3%) longer.

Wing lengths of 152-157mm for A♂ and 152-159mm for A♀ of Cooper & Forshaw (1977) are dramatically/exclusively shorter than ours for the former and near exclusively shorter for the latter sex.

1) *P. c. carunculata* Lesson, 1835. Histoire naturelle des oiseaux de paradis et des épimaques 1835: 242. Arfak Mts.

2) *P. c. intermedia* Ogilvie-Grant, 1913. Bulletin of the British Ornithologists' Club 31: 105. Utakwa R, Nassau Ra, at 5,500 ft. The status of the long problematical form *P. c. intermedia* has been recently discussed in detail, and we note here only that it is an invalid taxon as the only three known specimens have been shown to be relatively young individuals of *P. brevicauda* (Frith & Frith, in press). Its biometrical data are therefore included within *P. brevicauda*.

This species is distinctively different from *P. brevicauda* in size, relative proportions and in sexual dimorphism of these characters. Younger individuals of *carunculata* have a shorter tail than adults, whereas in *P. brevicauda* younger birds have a considerably longer one than adults.

#### *Paradigalla brevicauda* Short-tailed *Paradigalla* (Table 12)

*P. brevicauda* Rothschild & Hartert, 1911. Novitates Zoologicae 18: 159. Mt Goliath, central Dutch New Guinea. Monotypic. Synonym: *P. b. intermedia* (see *P. c. intermedia*). A♀ similar to or slightly smaller than A♂, MWL and MW by 5 & 6% respectively. MTCL only 2 & 1mm shorter than MTL in A♂ and A♀ respectively. A♀ MTL, however, is considerably longer (28%) than A♂. MTL of I♂ also much longer (47%) than A♂, and I♀ also have a longer (31%) tail than A♀ (sample small). Thus, ♂ acquire a progressively shorter (32%) tail, the central pair also

decreasing in relative length (35%) with age. MTL 34% of MWL in A♂, but 45% in A♀, so proportionately much longer in ♀. MLL of A♀ 5% longer than in A♂, but as a proportion of MWL the same. MBL similar in both sexes, but as a proportion of MWL negligibly (2%) longer in A♀ than A♂.

A stated average tail length of 90mm for this species is too long (*pace* Cooper & Forshaw, 1977).

***Ptiloris paradiseus* Paradise Riflebird**  
(Table 13)

*P. paradiseus* Swainson, 1825. Zoological Journal 1: 479. No type locality (= northern New South Wales). Monotypic. A♀ average smaller than A♂, MWL and MW (sample small) by 10 & 26% respectively. A♀ also slightly smaller (3%) in both MWL and MTL than I♂ and lighter (9%, but small sample). MTL of A♀ shorter (7%) than in A♂, but as a proportion of MWL negligibly (2%) longer. MTL of I♂ (sample small) also shorter (4%) than A♂. MTCL 4, 3 & 9% shorter than MTL in A♀, I♂ and A♂ respectively. Thus, ♂ acquire a slightly overall longer tail with age, unlike other *Ptiloris* species, but subsequent tail centrals decrease slightly in actual length with age. MLL of A♀ 3% shorter than in A♂, but as a proportion to MWL similar in both sexes. MBL of A♀ 8% longer than A♂ and as a proportion of MWL 7% longer.

For discussion of 'reversed' sexual dimorphism in bill length, see Frith (in press).

***Ptiloris victorinae* Victoria's Riflebird**  
(Table 14)

*P. victorinae* Gould, 1850. Proceedings of the Zoological Society of London 1849: 111. Barnard Is, North Queensland. Monotypic. A♀ average smaller than A♂, MWL and MW by 10 & 18% respectively. A♀ also slightly smaller in MWL and MTL (3 & 4%) than I♂ and lighter (7%). MTL of A♀ shorter (4%) than in A♂, but as a proportion of MWL slightly (4%) longer. MTCL only 3% shorter in A♀ and I♂, but 5% shorter in A♂. Thus, although very little variation in tail length between A♂ and I♂, tail centrals do decrease slightly in length with age. MLL of A♀ 6% smaller in A♂, but as a proportion of MWL similar in both sexes. MBL of A♀ 4% longer than A♂ and as a proportion of MWL 5% longer.

Cooper & Forshaws' (1977) A♀ tarsal length range of 34-39 mm is exclusively longer than we

found. For a discussion of 'reversed' sexual dimorphism in bill length, see Frith (in press).

***Ptiloris magnificus* Magnificent Riflebird**  
(Table 15)

A♀ markedly smaller than A♂, MWL and MW by 19 & 34% respectively. MWL of A♀ exclusively shorter than A♂. A♀ considerably smaller in MWL and MTL (12 & 8%) than I♂, and much lighter (27%) — more so than the other two *Ptiloris* species. MTL of A♀ shorter (3%) than in A♂, but as a proportion of MWL much (10%) longer. MTL of I♂ longer (7%) than A♂. MTCL and MTL similar in A♀ and I♂, but 5% shorter in A♂. Thus, ♂ acquire a progressively shorter (6%) tail, tail centrals decreasing (11%) in length at a greater rate with age. MLL and MBL of A♀ 10 & 11% shorter than in A♂ respectively, but as a proportion of MWL negligibly (2 & 3%) longer.

Tarsal lengths of Cooper & Forshaw (1977) are almost longer and are exclusively longer than ours for A♂ and ♀ respectively.

1) *P. m. magnificus* (Vieillot, 1819). Nouveau Dictionnaire d'Histoire Naturelle, nouvelle édition, 28: 167. 'Nouvelle Guinée', restricted to Dorey, Vogelkop.

2) *P. m. alberti* Elliot, 1871. Proceedings of the Zoological Society of London, p. 583. Cape York, Australia. MWL of A♂ c. 11mm shorter and MTL, MLL fractionally less, and bill narrower and conspicuously more decurved than in other two subspecies. Extent of culmen base feathering is intermediate between that of nominate *magnificus* and *intercedens*. MTCL of A♂ relatively shorter (8mm) than rest of tail than in other two subspecies (both 5mm).

3) *P. m. intercedens* Sharpe, 1882. Journal of the Linnean Society of London, Zoology 16: 444. Milne Bay and East Cape, south-eastern New Guinea. In almost all mean measurements of both sexes and all age classes this subspecies is all but identical to nominate except for MBL being c. 4mm less. Bill straighter than that of *alberti*.

There are striking differences in ♂ advertisement call between the subspecies (first noted by Hunstein, in Sharpe 1891) but also within the populations of *P. m. alberti* (pers. obs.). In *P. m. magnificus* and *P. m. alberti* the culmen is unfeathered along the ridge while in *P. m. intercedens* only a small proportion of the culmen base is unfeathered. The flank plumes in *P. m. magnificus* and *P. m. alberti* are longer than the tail but in *P. m. intercedens* they are equal to or shorter than the tail. In view of these differences it has

been suggested that *P. m. intercedens* might represent a distinct sibling species (Beehler & Swaby, 1991). Because the feathered condition of the culmen base in Australian *P. m. alberti* is intermediate between *intercedens* and nominate *magnificus* and that the Australian population exhibits considerable geographical variation in vocalization within its small range (MacGillivray, 1918; Frith & Beehler, in prep.; pers obs.), however, we here treat *intercedens* as a subspecies. A hybrid specimen between *P. m. intercedens* and *P. m. magnificus*, was collected at Putei (CSIRO 4112), just to the east of the Purari R. The subspecies *P. m. intercedens* is confined to the east of this river on the New Guinea south coast and *P. m. magnificus* otherwise known from well to the west of it (Beehler & Swaby, 1991).

**Semioptera wallacei** Standardwing Bird of Paradise (Table 16)

A ♀ average smaller than A ♂, MWL and MW by 8 & 17% respectively. MTL of A ♀ longer (5%) than in A ♂ and as a proportion of MWL 8% longer. MTL of I ♂ also longer (7%) than A ♂. MTL and MTCL similar in A ♀ and I ♂, but 15% shorter in A ♂. Thus, ♂ acquire a progressively shorter tail, tail centrals decreasing considerably (21%) in length and more so with age. MLL of A ♀ 6% shorter than in A ♂, but as a proportion to MWL similar in both sexes. MBL of A ♀ 3% shorter than in A ♂, but as a proportion of MWL negligibly (2%) longer. Standards average  $154 \pm 13$  mm ( $n = 58$ ) long in A ♂.

1) *S. w. wallacei* Gray, 1859. Literary Gazette (new series) 39: 406. Near Labuha Village, Bacchian (= Bacan) I.

2) *S. w. halmaherae* Salvadori, 1881. Ornithologia della Papuasie e della Molucche 2: Torino, p. 73. Halmahera. Similar to nominate but crown and nape (and in some individuals also mantle) with rich pinkish coppery-purple iridescence. MWL as in the nominate, MTL longer and other measurements slightly smaller.

**Seleucidis melanoleuca** Twelve-wired Bird of Paradise (Table 17)

A ♀ average slightly smaller than A ♂, MWL and MW by 6 & 11% respectively. MTL in A ♀ much (and exclusively) longer (49%) and as a proportion of MWL far greater (64%) than in A ♂ (40%). MTL of I ♂ similar to A ♀. MTCL negligibly shorter than MTL in both sexes and all ages. Thus, ♂ acquire a progressively and grossly

shorter (35%) tail with age. MLL and MBL of A ♀ 7 & 9% shorter than in A ♂ respectively, but similar in proportion to MWL in both sexes. MFPL  $266 \pm 35$  mm ( $n = 48$ ) in A ♂.

1) *S. m. melanoleuca* (Daudin, 1800). Traité d'Ornithologie (Lesson) 2: 278. Waigiou, in error for Salawati or the Vogelkop.

2) *S. m. auripennis* Schlüter, 1911. Falco 7: 2. Dallmannshafen (= Wewak), German New Guinea. Similar to but on average generally smaller (c. 6%), more so in MBL, than nominate and underparts of ♀ darker, more brownish, and more heavily barred.

**Epimachus albertisi** Buff-tailed Sicklebill (Table 18)

A ♀ similar to A ♂ in size and weight, MWL only 3% smaller. MTL of A ♀ also shorter (4%) and has the same (84%) proportionate length to MWL as A ♂. MTL of I ♂, however, negligibly (2%) longer than A ♂. Thus, surprisingly, ♂ decrease tail length very slightly with age, but data are equivocal. MLL similar in both sexes and in the proportion to MWL. MBL of A ♀ 4% longer than in A ♂ and as a proportion of MWL 3% longer.

Tail length and tail centrals of this species and *E. bruijnii* are of similar lengths in both sexes and all ages, and tail length is shorter than wing length. These two species, because of the consistent proportional and tail growth differences between them and the two larger *Epimachus* species (*fastuosus* and *meyeri*), were long treated as the separate genus *Drepanornis* (Gilliard, 1969). We here follow current usage (Diamond, 1972; Beehler & Finch, 1986; Beehler et al., 1986) but note the above differences suggest Cracraft (1992) was correct in treating *Drepanornis* as valid.

1) *E. a. albertisi* (Slater, June 1873). Nature 8: 151 and (1873) Proceedings of the Zoological Society of London p. 558, pl. 47. Hatam, Arfak Mts. MTL 87% of MWL in adults and proportionately longest in this subspecies.

2) *E. a. cervinicauda* Slater 1883. Proceedings of the Zoological Society of London, p. 578. Vicinity of Port Moresby. Upperparts in both sexes brown with slightest of chestnut suffusion, uppertail coverts and tail paler chestnut than in nominate. Underparts of ♀-plumaged birds pale buff barred strongly with paler brown than *albertisi*. Smaller than nominate. MTL 82% of MWL 82% in adults.

3) *E. a. geisleri* (Meyer, 1893). Abhandlungen und Berichte des Königlichen Zoologischen und Anthropologisch-Ethnographischen Museums zu Dresden 4: 15. Sattelberg, Huon Peninsula. MWL and MTL fractionally smaller than nominate; those of A♂ fall within the ranges given for the nominate but those of A♀ are exclusive, but samples too small ( $n = 9$ ) for meaningful comparisons. Diamond (1972), Cooper & Forshaw (1977), Coates (1990) and Cracraft (1992) concluded that *geisleri* should be combined with the nominate, notwithstanding the slightly smaller size of the former. We concur with this.

4) *E. a. inversus* Rothschild, 1936. Mitteilungen aus dem Zoologischen Museum, Berlin 21: 188. Mt Kunapi, Weyland Mts. Samples too small ( $n = 5$ ) for significant biometrical comparisons, but measurements similar to nominate. Diamond (1972), Cooper & Forshaw (1977), Coates (1990) and Cracraft (1992) concluded that *inversus* should be combined with the nominate, and we concur.

By synonymising *geisleri* and *inversus* with *albertisi*, MTL and MWL of both A♂ and A♀ of the resulting *albertisi* are still larger than those of *cervinicauda* and MTL 87% of MWL and proportionately still longer.

#### ***Epimachus bruijnii* Pale-billed Sickbill** (Table 19)

*E. bruijnii* (Oustalet, 1880). Annales des Scientifiques Naturelles, Paris ser. 6, 9, 1. and 1880 Bulletin de l' Association Scientifiques, France, p. 172. Coast of Geelvink Bay between 136°30' and 137° of longitude. Monotypic. A♀ similar to A♂ in size and weight, MWL and MW by 3 & 9% smaller respectively. MTL in adults of both sexes almost identical with a similar (69 & 70%) proportionate length to MWL. MTL of I♂, however, longer (5%) than A♂. Thus, surprisingly, ♂ tail length decreases very slightly with age, but data are equivocal. MLL and MBL of A♀ 3 & 5% shorter than in A♂ respectively, but as a proportion to MWL similar in both sexes.

The adult tail length of 16cm for the species by Cooper & Forshaw (1977) is far too long.

#### ***Epimachus fastuosus* Black Sickbill** (Table 20)

A♀ markedly smaller than A♂, MWL, MTL and MW by 15, 44 & 30% respectively. MTL of A♂ and A♀ 100 & 32% proportionately longer than MWL, as in *E. meyeri*. MTL of A♀ and I♂ 24 & 23% shorter than MTCL respectively, but

in A♂ this difference far greater (45%). Thus, ♂ acquire progressively longer tails with increasing age, the tail centrals more than doubling in length. MLL and MBL of A♀ 7 & 3% shorter than in A♂, but as a proportion of MWL slightly (3 & 5%) longer.

It is not true that I♂ can be told apart from ♀ in the field by their longer and thicker bills (*contra* Majnep & Bulmer 1977).

1) *E. f. fastuosus* (Hermann, 1783). Tabula affinitatum animalium (Argentorati), p. 195 (based on Daubenton, Planches Enluminées, pls 638-639). New Guinea, restricted to Arfak Mts (Hartert 1930).

2) *E. f. atratus* (Rothschild & Hartert), 1911. Novitates Zoologicae 18: 160. Mt Goliath, Oranje Mts, Dutch New Guinea. A♂ darker on underparts and A♀ more olive, less rufous, on uppertail than *fastuosus*. A♂ measurements similar to nominate, but some variation between A♀, notably in tail length (6% shorter).

3) *E. f. stresemanni* Hartert, 1930. Novitates Zoologicae 36: 34. Schraderberg, Sepik Mts. A♂ darker on underparts than nominate but a Leiden Museum specimen of *stresemanni* from Anggi Gita, Arfak Mts, is intermediate in this character. This subspecies is considerably larger than the nominate in every respect. It is also larger than *atratus*, with which it has been synonymised, MWL, MTL and MW (sample small) of A♂ being 9%, 17% & 18% longer respectively. This notwithstanding, the subspecies is considered invalid given observations of Gilliard & LeCroy (1961), Diamond (1969) and Cracraft (1992) concerning the clinal nature of otherwise on average larger *stresemanni*. When *stresemanni* is synonymised with *atratus*, however, the latter becomes a taxon of much larger individuals, still larger than the nominate.

4) *E. f. ultimus* Diamond, 1969. American Museum Novitates 2362: 31. Summit of Mt Menawa, Bewani Mts, Sepik District, Mandated Territory of New Guinea. Differs from nominate, but resembles *atratus* (and *stresemanni*), in being more black, less brown, on underparts of A♂ and more olive, less rufous, on uppertail of A♀. Bill nearly exclusively shorter (sample small) than individuals of other subspecies

#### ***Epimachus meyeri* Brown Sickbill** (Table 21)

A♀ markedly smaller than A♂, MWL, MTL and MW by 14, 20 & 29% respectively. MTL of A♂ and A♀ 39 & 28% longer than MWL respectively. MTL of A♀ and I♂ is 32 & 35% shorter

than MTCL respectively, but in A♂ 64%. Thus, ♂ acquire progressively longer tails with increasing age, the tail centrals more than doubling in length. MLL of A♀ 9% shorter than in A♂, but similar in proportion to MWL in both sexes. MBL of A♀ 3% longer than in A♂, but as a proportion of MWL 6% longer.

Cooper & Forshaws' (1977) tarsal lengths of 58-62mm and 51-59mm for nominate A♂ and ♀ respectively are much larger than we found, with those of the former sex exclusively so. It is not true that I♂ can be told apart from ♀ in the field by their longer and thicker bills (*contra* Majnep & Bulmer, 1977).

1) *E. m. meyeri* Finsch, 1885. Zeitschrift für die gesammte Ornithologie 2: 380. Hufeisengebirge, south-eastern New Guinea. Flank plumes are laven brown. A♂ and A♀ larger than other subspecies with respect to MWL, MTL, MTCL, MTL and MW.

2) *E. m. albicans* (Van Oort, 1915). Zoologische Mededelingen, Leiden 1: 228. Treubivak (2366m), Treub Mts, Central New Guinea. Like nominate but slightly smaller, and flank plumes of A♂ paler than both *meyeri* and *bloodi* in being white.

3) *E. m. megarhynchus* Mayr & Gilliard, 1951. American Museum Novitates 1524: 10. Gebroeders Mts, Weyland Ra, Dutch New Guinea, 6000-7000ft. The subspecies *megarhynchus* was erected on the basis of a larger bill than the others, but bill lengths of the only three specimens known (♂ 82, ♀ 79, 83mm) in fact fall within the range of all subspecies (see measurements); see also Cracraft (1992). This subspecies is now considered synonymous with *albicans* (Cracraft, 1992), with which we concur.

4) *E. m. bloodi* Mayr & Gilliard, 1951. American Museum Novitates 1524: 10. Mt Hagen, Central Highlands, Mandated Territory of New Guinea, 8300ft. Like nominate but a good deal smaller and lighter. Flank plumes of A♂ paler, more dirty whitish, than dirty pale brownish of *meyeri*.

#### *Astrapia nigra* Arfak *Astrapia* (Table 22)

*A. nigra* (Gmelin, 1788). *Systema Avium* 1: 401. 'Oceanic Islands', restricted to the Arfak Mts, New Guinea. Monotypic. A♀ slightly smaller than A♂, MWL by 8%. MTL 116 & 52% longer than MWL in A♂ and A♀ respectively. MTL in A♀ and I♂ shorter than in A♂ by 35 & 33% respectively. MTL of A♀, I♂ and A♂ 17, 19 &

30% shorter than MTCL respectively. Thus, ♂ tail length progressively increases considerably with age, MTL and MTCL increasing by 50 & 74% respectively. In this respect this species is similar to *A. rothschildi* and unlike their congeners. MLL of A♀ 4% shorter than in A♂, but similar in proportion to MWL in both sexes. MBL similar in both sexes, but as a proportion to MWL negligibly (2%) longer in A♀.

#### *Astrapia splendidissima* Splendid *Astrapia* (Table 23)

A♀ closer to A♂ in general size than most bird of paradise species, MWL similar but MW 11% less — unlike all congeners. MTL 27 & 39% longer than MWL in A♂ and A♀ respectively. MTL of A♀ and I♂ longer than A♂ by 8 & 12% respectively. MTL of A♀, I♂ and A♂ 11, 13 & 20% shorter than MTCL respectively. Thus, ♂ tail length decreases slightly with age, more so MTL (11% shorter) than MTCL (4% shorter). MLL of A♀ negligibly (2%) shorter than in A♂, but similar in proportion to MWL in both sexes. MBL similar in both sexes, and also as a proportion of MWL. It is presumably as a result of the reduced overall body size of this species that MBL is large proportionate to MWL (30%) compared to other *Astrapia* species (20-25%).

1) *A. s. splendidissima* Rothschild, 1895. Novitates Zoologicae 2: 59, pl. 5. 'Probably Charles-Louis Mts' but instead almost certainly from Weyland Mts (Mayr, 1941).

2) *A. s. helios* Mayr, 1936. American Museum Novitates 869: 3. Mt Goliath, Oranje Ra, Dutch New Guinea. Like the nominate but crown, neck and dorsal collar of A♂ more bluish and less golden-green, and spatulate tips of central tail feather pair broader. Female-plumaged birds slightly darker above. Birds of both sexes and all age classes differ from nominate by having extensive, unconcealed, white bases to underside of outer primaries except outermost two, this character being previously overlooked (Mayr, 1936; Gilliard, 1969; Cracraft, 1992). These characters and the fact that individuals of *helios* are on average larger than the nominate, particularly in overall tail length (central pair = 15mm longer in A♂ and 8mm in A♀), contradict Cracraft's (1992) view that *helios* is invalid.

3) *A. s. elliotsmithi* Gilliard, 1961. American Museum Novitates 2031: 3. Mt Ifal, 7,200ft asl, Victor Emanuel Mts, Mandated Territory of New Guinea. This subspecies resembles *helios*, but its tail is even longer (central pair = 17mm longer in

A♂ and 12mm in A♀). We agree with Cracraft (1992) in synonymising *elliottsmithi* with *helios* and concur with his reservations, as the slightly larger average size of this subspecies appears no more than the extreme of a west to east clinal increase in the species and because its white primary bases are of the *helios* kind and are unlike those of the nominate. Synonymising these two subspecies increases the average size of resulting *helios*, especially tail length, the central pair being 20mm longer in A♂ and 12mm in A♀ than in the nominate.

***Astrapia mayeri* Ribbon-tailed Astrapia**  
(Table 24)

*Astrapia mayeri* Stonor, 1939. Bulletin of the British Ornithologists' Club 59: 57. 'Eighty to a hundred miles west of Mt Hagen' [Station] = Mt Hagen, PNG.

A♀ markedly smaller than A♂, MWL and MW by 12 & 10% respectively. MTL 62 & 97% of MWL in A♂ and A♀ respectively. MTL of A♀ and I♂ longer than A♂ by 37 & 46% respectively. MTL of A♀, I♂ and A♂ 50, 46 & 88% shorter than MTCL respectively. Thus, MTL of A♂ decreases considerably in length with age (by 32%), whereas MTCL increase dramatically (198% longer). MLL of A♀ 4% shorter than in A♂, but as a proportion of MWL negligibly (2%) longer. MBL similar in both sexes, but as a proportion of MWL negligibly (2%) longer in A♀.

***Astrapia stephaniae* Stephanie's Astrapia**  
(Table 25)

A♀ on average slightly smaller than A♂, MWL and MW by 9% & 12% respectively. MTL only 85% MWL in A♂, but in A♀ 25% longer. MTL of A♂ shorter than A♀ and I♂ by 25 & 27% respectively. MTL of A♀, I♂ and A♂ 40, 43 & 77% shorter than MTCL respectively. Thus, MTL of A♂ decreases considerably with age (27% shorter), whereas MTCL increases (85% longer). In A♂, rectrices other than the central pair are not proportionately greatly reduced in length as in *A. mayeri*, but progressively decrease in length with age synchronously with grossly increasing central rectrices length. MLL of A♀ 4% shorter than in A♂, but as a proportion of MWL similar in both sexes. MBL similar in both sexes, but as a proportion of MWL slightly (3%) longer in A♀ than in A♂. MBL of both sexes much longer (13%), and also longer (3%) as proportion of MWL, than in the closely related *A. mayeri*.

1) *A. s. stephaniae* (Finsch & Meyer, 1885). Zeitschrift für die gesammte Ornithologie 2: 378. Hufeisengebirge.

2) *A. s. feminina* Neumann, 1922. Verhandlungen der Ornithologischen Gesellschaft in Bayern 15: 236. Schraderberg. MWL of A♂ slightly shorter (3%) than *stephaniae* but the same as in *ducalis* whereas MTL the same as *stephaniae* but larger than *ducalis*, but samples too small (n=2) for meaningful comparisons.

3) *A. s. ducalis* Mayr, 1931. Mitteilungen aus dem Zoologischen Museum, Berlin 17: 711. Dawong, Herzog Mts. Like nominate but less contrast between colour of crown/nape and the back, and the crown and nape more bluish-black. On average smaller than the nominate in all significant characters. Confusion over the supposed range of *feminina* (*sensu stricta*) exists: Gyldenstolpe (1955) and Coates (1990) included the Wahgi-Sepik Divide, which is considered by others to be occupied by *ducalis* (Mayr & Gilliard, 1952; Gilliard, 1969). We note Cracraft's (1992) observations and tentatively agree with him in relegating *ducalis* to synonymy with *feminina*, while noting their general overlap in measurements.

***Astrapia rothschildi* Huon Astrapia**  
(Table 26)

*A. rothschildi* Foerster, 1906. Two New Birds of Paradise: 2. Rawlinson Mts, north-eastern New Guinea. Monotypic. A♀ markedly smaller than A♂, MWL and MW (small sample) by 12% & 23% respectively. MTL as a proportion of MWL 87 & 33% longer in A♂ and A♀ respectively. MTL of A♂ shorter than those of A♀ and I♂ by 38 & 36% respectively. MTL of A♀, I♂ and A♂ 14, 12 & 21% shorter than MTCL respectively. Thus, ♂ tail length increases considerably with age, MTL & MTCL by 56 & 74% respectively. Unlike other *Astrapia* species, except *A. nigra*, rectrices other than the central pair do not decrease in length with age but become progressively longer as does the central pair. MLL of A♀ 4% shorter than in A♂, but as a proportion to MBL negligibly (2%) longer. MBL similar in both sexes, but as a proportion to MWL slightly (3%) longer in A♀ than A♂.

***Lophorina superba* Superb Bird of Paradise**  
(Table 27)

A♀ markedly smaller than A♂, MWL and MW by 12 & 23% respectively. A♀ also smaller than I♂, MWL, MTL and MW by 6, 3, & 12% respec-



tively. MTCL negligibly (1-2mm) longer than the outer rectrices in birds of all ages and sexes, and this is true for all subspecies. MTL shorter (7%) in A ♀, but as a proportion of MWL longer (3%) than in A ♂. MTL increases slightly (4%) with age in ♂, but data vary with subspecies. MLL of A ♀ 7% shorter than in A ♂, but as a proportion to MWL negligibly (2%) longer. MBL similar in both sexes, but as a proportion of MWL slightly (3%) longer in A ♀ than A ♂.

It is noteworthy that bill measurements of this species clearly illustrate a serious potential problem in measuring exposed culmen as opposed to bill length. Culmen measurements presented by Gilliard (1969) and Cooper & Forshaw (1977) suggest that the bill is longer in females than in males in this species. This is, however, an artifact of sexual dimorphism in the extent of forehead feathers and structure; in functional bill length *per se* there is no sexual dimorphism, while in proportionate bill length females are larger.

Complex subspeciation has long been debated, with various authors accepting different numbers of subspecies (Gilliard, 1969; Diamond, 1972; Coates, 1990; Cracraft, 1992). We list all subspecies below, compare their biometrical data and note which have been, or we consider should be, synonymised.

1) *L. s. superba* (Pennant, 1781). Specimen Faunula Indica, in Forster's Indian Zoology, p. 40 (based on Daubenton, Planches Enluminées, pl. 632). New Guinea, restricted to Arfak Mts. A ♀ blackish-brown on head and nape, except the chin and throat, with a short line of tiny whitish spots as a sub-obsolete, post-ocular, supercilium stripe. Mantle to upper tail coverts and wings dark red-brown. Upper tail fuscous with pale chestnut outer feather edging. Chin, throat and underparts pale buff to darker buff, uniformly and narrowly barred brownish-black. MTL 73 and 78% of MWL in A ♂ and A ♀ respectively. MWL and MTL of both sexes notably longer than in most other subspecies.

2) *L. s. minor* Ramsay, 1885. Proceedings of the Linnean Society of New South Wales 10: 242. Astolabe Mts, Mekeo, south-east New Guinea. A ♀ blacker plumaged than other subspecies, with head and throat blackish-brown and upperparts rich dark chestnut. No supercilium stripe in front of and above eye and sub-obsolete behind it. No or little pale nape marking. MTL 67 & 70% of MWL in A ♂ and A ♀ respectively. MWL of A ♂ and A ♀ shorter (6 & 8%) than in the respective sexes of the nominate, as is MTL (14 & 16%). MWL of A ♂ shorter than all other subspecies.

3) *L. s. latipennis* Rothschild, 1907. Bulletin of the British Ornithologists' Club 19: 92. Rawlinson Mts, Huon Peninsula. A ♀ head dark brown, chin and throat whitish, with broad whitish supercilium stripe, white streaking on forehead, crown and nape; upperparts variably olive-brownish. MTL 70 & 71% of MWL in A ♂ and A ♀ respectively. Overall smaller than nominate, being most similar in size to *connectens* and *addenda* with which Cracraft (1992) has synonymised it. MTL of A ♂ almost identical, but MTL longer than in *connectens* (4%) and *addenda* (7%).

4) *L. s. feminina* Ogilvie-Grant, 1915. Ibis, Jubilee Supplement 2: 27. Utakwa R, Nassau Ra. A ♀ similar in general appearance to *latipennis*, the broad supercilium stripes joining narrowly across the nape. MTL 63% & 66% of MWL in A ♂ and A ♀ respectively. Thus, wings are proportionately much longer relative to tail length than in other subspecies.

5) *L. s. niedda* Mayr, 1930. Ornithologische Monatsberichte 38: 179. Wondiwoi, and Wandammen Mts. A ♂ like nominate in appearance, but ♀ plumage with distinctly darker underparts being more ochraceous. MTL 73% of MWL in A ♂, but in A ♀ this figure much larger (82%), as in the nominate, but samples small. In general and proportionate measurements most like the nominate.

6) *L. s. connectens* Mayr, 1930. Ornithologische Monatsberichte 38: 180. Dawong, Herzog Mts. MTL 66 & 70% of MWL in A ♂ and A ♀ respectively. In general and proportionate measurements most like *addenda*, and similar to *latipennis*. Female plumage like *latipennis*. Considered virtually indistinguishable from *latipennis* by Diamond (1972), who considered it a synonym, and was followed by Cracraft (1992). We concur with Cracraft (1992) that *connectens* and *addenda* be synonymised with *latipennis* (see below).

7) *L. s. sphinx* Neumann, 1932. Ornithologische Monatsberichte 40: 121. One (type) ♀-plumaged specimen only for which the locality is unknown. Gilliard (1969) recognised this as a distinct subspecies with 'More reddish brown on upperparts than *minor*. Eyestripe less extensive and forehead and neck without white flanks'. Wing and tail lengths are markedly longer than those of *minor* and more like those of *latipennis*. Cracraft (1992) synonymised *sphinx* with *minor*, an action as acceptable as any. We note that the presence of *L. superba* on the Hunstein Ra is indicated by the hybrid *L. superba* x *P. carolae* previously known as *L. s. pseudoparotia* (Frith & Frith, 1996b). It is



therefore possible the type specimen of *sphinx* is from the Hunstein Ra (its measurements are in fact closer to those of geographically closest *addenda*).

8) *L. s. pseudoparotia* Stresemann, 1934. Ornithologische Monatsberichte 42: 144. Hunsteinspitze, middle Sepik. Until our visit to the Zoologisch Museum, Berlin, this subspecies was still recognised (Gilliard, 1969; Diamond, 1972; Cooper & Forshaw, 1977; Cracraft, 1992); however, the unique type specimen is, in fact, an individual resulting from the hybridization of *Lophorina superba* and *Parotia carolae* in the Hunstein Ra (Frith & Frith, 1996b). No other specimen of (normal) *L. superba* is known from this mountain range. The biometrical data of *pseudoparotia* are therefore excluded from Table 27.

9) *L. s. addenda* Iredale, 1948. Australian Zoologist 11: 162. Mt Hagen district. A ♀ plumage like *feminina* and *latipennis* but with some differences (Gilliard, 1969). MTL 65 & 70% of MWL in A♂ and A♀ respectively. Similarly size to *latipennis*, although MTL in A♂ 6% shorter. In general and proportionate measurements it is most like *connectens*, however. Placed in the synonymy *L. s. latipennis* by Cracraft (1992) on plumage morphology.

10) *L. s.* subspecies. We measured four individuals, one A♂, one SA♂ (with 15% A♂ plumage but otherwise in female plumage) and two A♀, from Wanuma, Adelbert Mts, Madang district. We, like Pratt (1982), could not assign these to a subspecies and they are much larger than any other taxon measured. Wing, tail, tarsal, bill lengths and bill width measured 144, 95, 33.5, 29.6 & 5.9mm in the A♂ and averaged 124, 84, 29.7, 29.5 & 6.3mm in A♀ (n = 2) respectively. As in other subspecies, the tail centrals of A♂ and A♀ are slightly longer (5 & 3mm respectively) than the remainder of the tail. A♂ wing and tail lengths are notably long, but the sample too small for meaningful comparison.

With regard to the validity of taxa in this species those accepted by Cracraft (1992) broadly agree with some or most doubts expressed by Gilliard (1969), Diamond (1972) and Coates (1990). Until such time as a comprehensive re-evaluation of its systematics indicates otherwise, we accept the following subspecies: *L. s. superba*, *niedda*, *minor* (*sphinx*), *latipennis* (*connectens*, *addenda*), *feminina*, with synonyms given in parentheses. *L. s. pseudoparotia* is invalid as detailed above.

#### *Parotia wahnesi* Wahnes' Parotia (Table 28)

*P. wahnesi* Rothschild, in Foerster & Rothschild, 1906. Two New Birds of Paradise: 2 Rawlinson Mts. Monotypic. A ♀ smaller than A♂ in MWL (almost exclusively so) and MW (sample small), by 7 & 15% respectively. MTL as a proportion of MWL 16 & 3% longer in A♂ and A♀ respectively, unlike all other *Parotia* species. MTL considerably shorter than MTCL, by 8% shorter in both A♀ & I♂ and 12% in A♂. MTL and MTCL in A♀ shorter (18 & 22% respectively) than A♂, the central pair exclusively so. MTL of I♂ longer (5%) than A♀, but shorter (18%) than A♂. Thus, ♂ tail length increases with age, MTCL more so (22%) than MTL (16%). MLL of A♀ 9% shorter than in A♂, but as a proportion of MWL similar in both sexes. MLL, as in all *Parotia* species, proportionately long for a typical bird of paradise, averaging 32% of MWL in A♂. MBL similar in both sexes, but as a proportion of MWL negligibly (2%) longer in A♀ than A♂. MOPL of A♂ average  $138 \pm 4$ mm (n = 18). METL of A♂ longer ( $25 \pm 4$ mm, n = 15) than I♂ ( $15 \pm 1$ mm, n = 7) and A♀ ( $15 \pm 2$ mm, n = 17).

#### *Parotia sefilata* Western Parotia (Table 29)

*P. sefilata* (Pennant, 1781). Specimen Faunula Indica, in Forster's Indian Zoology, p. 40. New Guinea, restricted to Arfak Mts. Monotypic. A ♀ smaller than A♂ in MWL (almost exclusively so) and MW, by 8 & 10% respectively. MTL 77 & 84% of MWL in A♂ and A♀ respectively. MTCL negligibly (1-3mm) longer than MTL in birds of all ages and sexes. MTL and MTCL of A♂ and A♀ similar, but I♂ 5% longer than adults of both sexes. I♂ 5% longer than adults of both sexes. Thus, ♂ tail length decreases slightly (4%) with age. MLL of A♀ 10% shorter than in A♂, but as a proportion of MWL similar in both sexes, averaging 32%. MBL similar in both sexes, but as a proportion of MWL negligibly (2%) longer in A♀ than A♂. Occipital plumes of A♂ average  $175 \pm 3$ mm (n = 29). METL of A♂ longer ( $30 \pm 3$ mm, n = 28) than I♂ ( $16 \pm 1$ mm, n = 16) and A♀ ( $15 \pm 1$ mm, n = 24).

#### *Parotia carolae* Carola's Parotia (Table 30)

A ♀ smaller (7%) than A♂ in MWL (almost exclusively so) and considerably lighter (37%).

suggesting a far greater sexual dimorphism in weight, but samples too small for meaningful conclusions. MTL 50 & 64% of MWL in A♂ and A♀ respectively, MTL and MTCL similar in length in birds of all ages and sexes. MTL of A♀ and I♂ 19 & 25% longer than in A♂ respectively. Thus, ♂ tail length decreases considerably (20%) with age, MLL of A♀ 8% shorter than in A♂, but as a proportion of MWL similar in both sexes and averages 33%. MBL 6% longer in A♀ than in A♂, unlike other *Parotia* species, and as a proportion of MWL slightly (3%) longer. MOPL of A♂  $122 \pm 7$  mm ( $n = 28$ ). METL of A♂ longer ( $22 \pm 2$  mm,  $n = 11$ ) than I♂ ( $12 \pm 1$  mm,  $n = 7$ ) and A♀ ( $12 \pm 1$  mm,  $n = 42$ ).

This species presents a complex, and one of the most interesting, problems of intraspecific variation, which requires considerably more collecting over its range before a satisfactory study can be undertaken. The subspecific biometrics do not help greatly as sample sizes are small, the characters do not vary greatly in size between the subspecies, and relative proportions of MTL, MTL and MBL to MWL are remarkably similar throughout the species.

1) *P. c. carolae* Meyer, 1894, Bulletin of the British Ornithologists' Club 4: 6. Amberno R (but apparently in fact Weyland Mts). MOPL  $117 \pm 3$  mm ( $n = 11$ ).

2) *P. c. berlepschi* Kleinschmidt, 1897. Ornithologische Monatsberichte 5: 46. New Guinea. The Van Rees Mts of Irian Jaya have been suggested as the unknown home of this distinct subspecies (Mayr, 1962) as has the Foja Mts, Irian Jaya (Diamond, 1985). Only four specimens are known. Like nominate in size and appearance but upper neck, nape and mantle heavily bronzed and with throat black and spatulate tips to occipital plumes relatively very small; MOPL  $126 \pm 1$  mm ( $n = 2$ ).

3) *P. c. meeki* Rothschild, 1910. Bulletin of the British Ornithologists' Club 27: 35. Setekwa R. Dutch New Guinea. Like nominate in size and appearance but chin and sides of throat blackish and ♂ bill longer (near exclusively so, but sample small). MOPL  $119 \pm 10$  mm ( $n = 4$ ).

4) *P. c. chalcothorax* Stresemann, 1934. Ornithologische Monatsberichte 42: 145. Doormanpaad, upper Mamderano (Idenburg R). Like nominate but upperparts with bright coppery sheen, underparts more coppery and long loreal feathering less intense black, being slightly brownish. MWL of A♂ exclusively longer than the nominate, but samples small. Occipital plumes long, averaging  $121 \pm 4$  mm ( $n = 2$ ).

5) *P. c. chrysenia* Stresemann, 1934. Ornithologische Monatsberichte 42: 147. Lönberg, Sepik Mts. Traditionally said to differ from nominate by having the long black loreal feathering with a coppery sheen (like eye ring but darker), but several specimens lack this character, their lores being pure black. MWL and MTL of A♂ longer than the nominate, but samples too small for meaningful comparisons. Occipital plumes long, averaging  $131 \pm 8$  mm ( $n = 2$ ).

6) *P. c. clelandiae* Gilliard, 1961. American Museum Novitates 2031: 5. Telefomin 5000 ft. (1524 m), Victor Emanuel Mts, Mandated Territory of New Guinea. Like nominate but upperparts darker, more jet-black, less brown and on average larger, and A♂ bill slightly shorter. Occipital plumes long, averaging  $126 \pm 7$  mm ( $n = 7$ ).

#### *Parotia lawesii* Lawes' *Parotia* (Table 31)

A♀ slightly smaller than A♂, MWL and MW by 5 & 14% respectively, MTL as a proportion of MWL 66 & 52% in A♂ and A♀ respectively. MTL and MTCL similar in length in birds of all ages and sexes. MTL of A♀ and I♂ 23 & 24% larger than A♂. Thus, ♂ tail length decreases in length slightly with age. MLL and MBL of A♀ are 7 & 2% shorter than in A♂ respectively, but as a proportion of MWL similar in both sexes and averages 31%. MBL proportionately similar in both sexes. MOPL of A♂  $162 \pm 7$  mm ( $n = 58$ ). METL of A♂ longer ( $30 \pm 4$  mm,  $n = 32$ ) than I♂ ( $14 \pm 2$  mm,  $n = 26$ ) and A♀ ( $15 \pm 1$  mm,  $n = 37$ ).

The subspecific biometrics do not help greatly as the characters do not vary much in size between the subspecies and the relative proportions of MTL, MLL and MBL to MWL are remarkably similar throughout.

1) *P. l. lawesii* Ramsay, 1885. Linnæan Society of New South Wales 10: 243. Astrolabe Mts. MOPL of A♂  $160 \pm 5$  mm ( $n = 21$ ).

2) *P. l. helenae* De Vis, 1897. Ibis p. 390. Neneba, upper Mamhare R, north of Mt Strathley. Differs from nominate in A♂ forecrown being bronzed-brown, not silver-white, and in ♀ being slightly less red. All measurements of both sexes near-identical to nominate. MOPL of A♂  $161 \pm 7$  mm ( $n = 10$ ). Originally described as a distinct species and subsequently long considered a subspecies of *P. lawesii* until Schodde & McKean (1973) and Cracraft (1992) resurrected it as a species. We concur with Gilliard (1969), Diamond (1972),

Beehler & Finch (1985), Beehler et al. (1986) and Coates (1990), however, in treating it as *P. l. helenae*.

3) *P. l. fuscior* Greenway, 1934. Proceedings of the New England Zoological Club 14: 2. Mt Missim, Morobe district (Schodde & McKean, 1973; Cracraft, 1992). A♂ like nominate but ♀ said to be duller, less-chestnut brown above and with a darker head than *livesli* (Gilliard, 1969), when there is in fact much variation within the species. Measurements are entirely compatible with those of nominate. MOPL of A♂  $169 \pm 10$  mm ( $n = 7$ ). We concur with Schodde & McKean (1973) and Cracraft (1992) that this subspecies is invalid and is a synonym of the nominate.

4) *P. l. exhibitu* Iredale, 1948. Australian Zoologist 11: 162. Mt Hagen district. MOPL of A♂  $163 \pm 7$  mm ( $n = 10$ ). A♂ said to be like nominate but with darker sides to head and ventrally more uniformly barred (Gilliard, 1969) but variation within the species makes this diagnosis inadequate. Measurements are entirely compatible with those of nominate and, thus, it should be synonymised with it, in accord with Diamond (1972), Schodde & McKean (1973), Coates (1990) and Cracraft (1992).

#### *Pteridiphora alberti* King of Saxony Bird of Paradise (Table 32)

A ♀ slightly smaller than A♂, MWL and MW by 9 & 11% respectively. MTL negligibly (2%) shorter in A♀, but as a proportion of MWL sexually dimorphic, 73% in A♀ and 68% in A♂. MTL of I♂ negligibly (2%) longer than in A♂. Thus, ♂ tail length decreases slightly with age. MLL of A♀ 5% shorter than in A♂, but as a proportion of MWL similar in both sexes. MBL similar in both sexes, but as a proportion of MWL negligibly (2%) longer in A♀. MOPL of A♂  $410 \pm 42$  mm ( $n = 37$ ). METL of A♀ & I♂  $17 \pm 2$  mm ( $n = 46$ ).

1) *P. a. alberti* Meyer, 1894. Bulletin of the British Ornithologists' Club 4: 11. 'Mountains on the Ambero R', but apparently from Weyland Mts.

2) *P. a. burgersi* Rothschild, 1931. Novitates Zoologicae 36: 253. Schraderberg, Sepik Mts. occipital plumes of A♂ notably larger than in the other two subspecies, MOPL  $452 \pm 43$  mm ( $n = 3$ ), but sample small for meaningful comparison.

3) *P. a. hallstromi* Mayr & Gilliard, 1951. American Museum Novitates 1524: 12. Forests above Tomba, south slope of Mt Hagen, Central

Highlands, Mandated Territory of New Guinea. Birds have on average longer wings (4%,  $n = 68$ ) and tail (5%,  $n = 69$ ) than the two other subspecies, which are almost identical in size, ( $n = 76$ ), but overlap in ranges of measurements is considerable.

We concur with comments of Gilliard & LeCroy (1968), Diamond (1972), Coates (1990) and Cracraft (1992) concerning the difficulties of adequately differentiating the supposed subspecies and therefore consider *P. alberti* a monotypic species.

#### *Cicinnurus regius* King Bird of Paradise (Table 33)

A ♀ average the same size as A♂, their MWL being similar but MW 4% lighter. MTL of A♀ considerably longer (75%) than in A♂ and as a proportion of MWL 25% longer. MTL of I♂ similar to A♀. MTL 4 & 7% shorter than MTCL in A♀ and I♂ respectively, but 80% shorter in A♂. Thus, ♂ acquire progressively shorter outer tail rectrices with age, while simultaneously gaining a progressively grossly longer central pair. MBL and MLL and their proportion of MWL similar in both sexes.

Central rectrices of SA♂ show immense variation. Some ♀-plumaged birds, with only traces of A♂ plumage, had normal ♀-length central rectrices or far longer narrowly-pointed ones, often with slightly curved tips. In other SA♂, with a greater proportion of A♂ plumage, centrals were more wire-like with spatulate tips, which were slightly, half or distinctly curled. Some individuals even had two very different central rectrices: one long ♀-shaped one, which may or may be curved, and a much-longer wire-like spatulate-tipped one. Near-adult plumaged SA♂ often had one central rectrice tipped with a fully coiled green disc and the other hardly coiled with no green.

The biometrics do not help systematic assessments as characters do not vary greatly in size between the subspecies, and the relative proportions of MTL, MLL and MBL to MWL are remarkably similar throughout the species. The systematic treatment of intraspecific variation has been the subject of recent debate. Six subspecies had been long established (Mayr 1941, 1962). Gilliard also (1969) maintained six subspecies but pointed out that they are all very similar.

1) *C. r. regius* (Linnaeus, 1758). Systema Naturae, ed. 10, p. 110. East Indies (= Aru Is - of Berlepsch 1911 Abhandlungen Senkenberg-

ischen Naturforschender Gesellschaft 34: 59). Only known from the Aru Is. MWL, MTL and MBL of A♂ and A♀ longest in this form, but there is considerable overlap in size ranges with other subspecies. A♂ central rectrices are also long, and in this respect are most like *rex* and *gymnorhynchus*.

2) *C. r. rex* (Scopoli, 1786). *Deliciae Florae et Faunae Insubricae* (Ticini) pt. 2, 88 (based on Sonnerat 1776, *Voyage Nouvelle Guinea*, p. 156, pl. 95). 'New Guinea' = Sorong District, Vogelkop. Now known from Misol and Salawati Is and New Guinea except between Geelvink Bay and the Huon Gulf. Frequently reported to occur on Batanta I but probably erroneously (Mees, 1982). Slightly smaller than the otherwise similar nominate in MWL, MTL and MBL. Most similar in size to *gymnorhynchus*.

3) *C. r. coccineifrons* Rothschild, 1896. *Novitates Zoologicae* 3: 10. Jobi I (= Yapen I). Only known from Yapen I. In most measurements similar to birds of adjacent mainland (*cryptorhynchus*). MBL smaller (8%) than the nominate, being most like *similis* and *cryptorhynchus*.

4) *C. r. similis* Stresemann, 1922. *Journal für Ornithologie* 70: 405. Stephansort, Astrolabe Bay. Occurs only from Astrolabe Bay and the upper Ramu R west to at least Humboldt Bay and upper Memberamo R. This form generally smaller than all other subspecies in MWL, MTL, MBL and MLL being most like, but slightly smaller than, *cryptorhynchus* in sizes. MTCL 11mm shorter than nominate.

5) *C. r. cryptorhynchus* Stresemann, 1922. *Journal für Ornithologie* 70: 405. Taua, lower Mameramo R. Now known from eastern coast of Geelvink Bay and at north New Guinea near the Memberamo R mouth only. Most similar in sizes to *similis*. MTCL 6mm shorter than nominate.

6) *C. r. gymnorhynchus* Stresemann, 1922. *Journal für Ornithologie* 70: 405. Hedsbachküste near Finschhafen. Now known from north-east coastal Huon Gulf. On average generally smaller and most similar in size to *rex* overall.

Although birds on the Aru Is. (*C. r. regius*) are on average slightly larger than birds of southern New Guinea (*C. r. rex*), variation is great and slight differences in plumage morphology are inadequate to justify an Aru Is subspecies (Mees, 1964; Cracraft, 1992). Gilliard (1969), Diamond (1972), Cooper & Forshaw (1977) and Cracraft (1992) also pointed out the weak morphological differentiation of most populations. Mees (1964, 1965, 1982) suggested that only two subspecies,

*C. r. regius* (including *rex* and *gymnorhynchus*) and *C. c. coccineifrons* (including *cryptorhynchus* and *similis*) be retained and that the roundish spot of green feathers above the eye of the former and the more elongate one in the latter be a 'tolerably constant character'.

More recently Cracraft (1992) recognised four subspecies (species in his view) but we find Cracraft's criteria inconsistent (e.g., he synonymises *gymnorhynchus* into *regius* stating it is 'nearly 100% diagnosably distinct' but retains three taxa of the *coccineifrons* group because he viewed them as 'nearly 100% diagnosable'). We do not find Cracraft's (1992) tentative plumage characters in support of retaining *cryptorhynchus* as distinct convincing. Furthermore all measurements of that population are entirely comparable with those of Yapen I. (*coccineifrons*) and northern New Guinea (*similis*) populations. In fact almost all measurements of the three populations, *coccineifrons*, *cryptorhynchus* and *similis*, are clinal from larger to slightly smaller, west to east. The more easterly population of *gymnorhynchus* does not fit this pattern, however, having a larger bill and therefore being more like birds of southern New Guinea (*C. r. regius*).

Thus, we feel Mees (1964) should be followed in combining these taxa into two subspecies *C. r. regius* and *C. r. coccineifrons*. By so doing, A♂ and A♀ of the two subspecies are almost identical in size, except in tail measurements. There still exists considerable overlap in size ranges of all parameters between the two subspecies, however. MWL of A♂ of the enlarged *C. r. regius* (including *rex* and *gymnorhynchus*) is a negligible 2% longer than the enlarged *C. r. coccineifrons* (including *cryptorhynchus* and *similis*) and MTL are the same. MTCL and MBL in A♂ *C. r. regius*, however, 6 & 7% longer respectively than in *C. r. coccineifrons*, and 5 & 2% larger as a proportion of respective MWL.

#### ***Cicinnurus magnificus* Magnificent Bird of Paradise (Table 34)**

A♀ average slightly smaller than A♂, MWL and MW by 4 and 15% respectively. MTL of A♀ considerably longer (51%) than in A♂ and as a proportion of MWL 20% longer. MTL of I♂ similar to A♀. MTL only 2 & 5% shorter than MTCL in A♀ and I♂ respectively, but 86% in A♂. Thus, ♂ acquire progressively shorter rectrices with age, while simultaneously gaining a progressively grossly longer central pair. MLL of A♀ 5% shorter than in A♂, but as a proportion

of MWL similar in both sexes. MBL similar in both sexes and as a proportion of MWL.

The central rectrices of SA♂ show great variation, relative to the degree of A♂ plumage acquired (as described for *C. regius*). The biometrics do not help much as the various characters vary little in size between the subspecies and the relative proportions of MTL, MLL, and MBL to MWL are remarkably similar throughout the species.

1) *C. m. magnificus* (Pennant, 1781). Specimen Faunulae Indicae, in Forster's Indian Zoology, p. 40 (based on Daubenton, Planches Enluminées, pl. 631). Arfak Mts, Vogelkop.

2) *C. m. chrysopterus* (Elliot, 1873). Monograph of the Birds of Paradise, p. 13. Jobi I (= Yapen I, Irian Jaya). In all measurements of both sexes *chrysopterus* almost identical to nominate, except for longer (9%) MTCL of A♂. Also differs from nominate in its secondary coverts and outer edges of flight feathers being more orange, less yellow, and the crown darker.

3) *C. m. hunsteini* (Meyer, 1885). Zeitschrift für die gesammte Ornithologie 2: 389, pl. 21. Hufeisengebirge, southeastern New Guinea (= near Astrolabe Mts). Like nominate but paler on head and back (Gilliard, 1969), and orange on secondary coverts and outer edge of flight feathers brighter and deeper. All measurements of both sexes nearly identical to other subspecies, although the MWL in A♂ and A♀ slightly shorter by 3 & 4% respectively.

4) *C. m. intermedius* (Hartert, 1930). Novitates Zoologicae 36: 36. Snow Mts (= Upper Setakwa R, Irian Jaya). Like nominate but the scapulars and inner secondaries brighter, more dull orange than brown (Gilliard, 1969). In view of all measurements of both sexes of *intermedius* being extremely similar to *chrysopterus*, and of comments by Cracraft (1992), this subspecies should be synonymized with the former. MTCL of A♂, however, shorter (13%) than *chrysopterus*.

#### ***Cicinnurus respublica* Wilson's Bird of Paradise (Table 35)**

*C. respublica* (Bonaparte, 1850). Compte Rendu des séances de l'Académie des Sciences, Paris 30, 131-291. 'New Guinea', restricted to Waigeu I. Monotypic. A♀ average the same size or slightly smaller than A♂, MWL similar but MW 8% lighter. MTL of A♀ considerably longer (36%) than in A♂ and as a proportion of MWL 15% longer. MTL of I♂ similar to A♀. MTL and MTCL similar in A♀ and I♂, but in A♂ MTL

72% shorter than MTCL. Thus, ♂ acquire progressively shorter rectrices with age, while simultaneously gaining a progressively grossly longer central pair. MLL of A♀ negligibly (2%) shorter than in A♂, but as a proportion of MWL is similar in both sexes. MBL is similar in both sexes and as a proportion of MWL.

The central rectrices of SA♂ show great variation relative to the degree of A♂ plumage acquired (as described for *C. regius*).

#### ***Paradisaea raggiana* Raggiana Bird of Paradise (Table 36)**

A♀ smaller than A♂, MWL and MW by 13 & 36% respectively. MTL of A♀ also shorter (11%) than A♂, but as a proportion of MWL negligibly (2%) longer. MTL of A♀ and I♂ 7% longer than MTCL, but in A♂ 71% shorter. ♂ do not acquire significantly longer outer rectrices with age, I♂ only 4% shorter than A♂, but do gain a progressively grossly longer central pair. MLL of A♀ 11% shorter than in A♂, but as a proportion of MWL similar in both sexes. MBL of A♀ 4% shorter, but as a proportion of MWL negligibly (2%) longer. MFPL of A♂ averages  $214 \pm 57$  mm ( $n = 96$ ).

The central rectrices of SA♂ of all *Paradisaea* species show immense variation. Some ♀-plumaged ♂, with only traces of adult plumage, have normal-length ♀-like central rectrices or far longer narrow and pointed ones, often slightly curved at their tips. Other SA♂, showing a greater degree of A♂ plumage, have thin long feathery central rectrices, often with feathery spatulate tips, or adult-like wires with spatulate tips.

The systematics of this species has been somewhat confused as it was long thought to represent a subspecies of the Greater Bird of Paradise, *Paradisaea apoda*. The establishment of common names for what earlier ornithologists considered species, but are now considered subspecies of *P. raggiana*, compounded the confusion. With respect to the (nominal) species, the mean measurements are so similar overall as to be of little diagnostic use, particularly as samples of the nominate are small. Variation in plumage markings and colouration is far more helpful.

1) *P. r. raggiana* Sclater, 1873. Proceedings of the Zoological Society of London, p. 559. Orangerie Bay. Now known from south-eastern New Guinea (Orangerie Bay to Milne Bay). The fore-back is yellow, fading as it overlays sepia of the mantle. Flank plumes of A♂ scarlet, MFPL

258 ± 74mm (n = 8). The average tail length of 15cm by Cooper & Forshaw (1977) for the nominate form is excessively long.

2) *P. r. augustaeivictoriae* Cabanis, 1888. *Journal für Ornithologie* 36: 119. 'Kaiser Wilhelm's Land', restricted to Finschhafen. Now known from the coast of Huon Gulf, the Markham R, and the headwaters of the Ramu R (at the Uria R). This subspecies averages overall c. 4% smaller than nominate, but there is considerable overlap in size ranges. Flank plumes of A♂ orange, MFPL 204 ± 51mm (n = 33), and c. 20% shorter than in nominate. Like *intermedia* but flank plumes orange, abdomen/belly paler, and yellow throat collar narrow.

3) *P. r. intermedia* De Vis, 1894. *Annual Report on British New Guinea*, 1893-94, p. 105. Kumusi R. Now known from Collingwood Bay to Holnicote Bay, Kumusi R, and the lower Mambare R. Like *salvadorii* but both sexes with yellow mantle/back and yellow streaking down to upper tail coverts. MWL and MTL of A♂ shorter than nominate and most like *augustaeivictoriae* in size. Flank plumes of A♂ scarlet and long, MFPL 239 ± 44mm (n = 18).

4) *P. r. granti* North, 1906. *Victorian Naturalist* 22: 156. 'German New Guinea'. Exact range unknown but somewhere between the Mambare R and Salamaua (= Morobe area). An examination of the majority of pertinent specimens proved confusing owing to considerable variation and lack of localities. Given the now better-defined southeastern-most distribution of *augustaeivictoriae* and the northwestern-most *intermedia*, we concur entirely with Rothschild (1930) and Mayr (1941, 1962) that *granti* is a changing, intergrading, population between the two (*contra* Cracraft, 1992). Only four A♂ measured as many specimens lack a location. MWL, MTL, MTCL, MLL, MBL and MBW 187, 131, 457, 40.4, 37.1 & 10.6mm respectively. Flank plumes of A♂ vary between the scarlet of *intermedia* and orange of *augustaeivictoriae*, MFPL 238 ± 47mm (these biometric data are excluded from Table 36).

5) *P. r. salvadorii* Mayr & Rand, 1935. *American Museum Novitates* 814: 11. Vanumai, Central Division, Papua, south-east New Guinea. Now known from south New Guinea from near the Papuan-West Irian border (Tarara), upper Fly and Purari valley (including the Wahgi). Like nominate but sepia mantle of both sexes lacking yellow, and scarlet of flank plumes less deep. Cracraft (1992) found evidence of clinal variation in characters of *salvadorii*. Similar in mean mea-

surements to nominate, but MTCL of A♂ 16mm longer and MFPL slightly shorter (201 ± 58mm, n = 37). The subspecies may be invalid. Further studies are required.

#### *Paradisaea apoda* Greater Bird of Paradise (Table 37)

A♀ smaller than A♂. MWL by 17%. Few weights available for this widely known species and none for adults. MTL of A♀ also shorter (14%) than A♂, but as a proportion of MWL slightly (3%) longer. MTL similar to MTCL in A♂, but 6% longer in A♀ and 75% shorter in A♂. ♂ do not acquire longer outer rectrices with age, A♂ only 9% shorter than A♂, but gain a progressively grossly longer central pair. MLL of A♀ 13% shorter than in A♂, but as a proportion of MWL similar in both sexes. MBL of A♀ also 5% shorter, but as a proportion of MWL 3% longer. MFPL 196 ± 56mm (n = 31).

Central tail rectrices of SA♂ show great variation, as in *P. raggiana*.

Gilliard's (1969) average A♂ tarsal length of 57mm for the species is presumably erroneous as it is exclusively longer than ours, and Cooper & Forshaw's (1977) tarsal lengths for nominate are extremely long, being exclusively longer than ours for A♀.

Considerable confusion exists in the synonymy of this species and that of *P. raggiana* because the latter was long treated as a subspecies of *P. apoda*. The considerable differences in size, ♀ plumage and head and back and flank plume markings and colouration in A♂ leave few doubts that the present treatment is correct, particularly as *P. apoda* does not intergrade with *P. raggiana*, but merely produces odd hybrid individuals where they meet. Two subspecies of *P. apoda* have long been established and widely accepted, but Cracraft (1992) suggested that the two forms are not diagnostically distinct with respect to the supposed paler and more maroon upper breast of *P. a. novaeguineae*. He apparently did not take the clearly different sizes of the two populations into account, the mainland birds being much smaller than those of the Aru Is. with no or little overlap in size (LeCroy, 1981). We accept both subspecies.

1) *P. a. apoda* Linnaeus, 1758. *Systema Naturae*, ed. 10, 1: 110. 'India' (= Aru Is, Irian Jaya). Only known from the Aru Is. MFPL of A♂ 210 ± 7mm (n = 14).

2) *P. a. novaeguineae* D'Albertis & Salvadori, 1879. *Annali Museo Civico Genova* 14: 96. Mid-



dle Fly R (300-450 miles upstream). This mainland subspecies has been long accepted on the basis of resembling the nominate but with the upper breast paler and more maroon and being smaller. MWL and MTL of A♂ and A♀ 11 & 14% and 12 & 16% shorter than nominate respectively. MLL and MBL of A♂ and A♀ also less, by 11 & 16% and 8 & 9% respectively. Moreover, MWL of A♀ as a percentage of A♂ in the nominate is 88% and MTL 93%, whereas in ♂ *novaeguinea* the respective proportions are 85 & 88%. MFPL of A♂  $185 \pm 40\text{mm}$  ( $n = 18$ ).

Cracraft (1992) considered supposed plumage characters not diagnosably distinct. We found mainland A♀ to be (almost exclusively) smaller than nominate A♀ in wing and tail length and to average a good deal smaller than the allopatric island nominate population in other measurements. We therefore retain the subspecies *novaeguinea*.

#### **Paradisaea minor** Lesser Bird of Paradise (Table 38)

A♀ smaller than A♂, MWL and MW by 15 & 35% respectively. MTL of A♀ also shorter (12%) than in A♂, but as a proportion of MWL negligibly (2%) longer. MTL of A♀ and I♂ 8 and 5% longer than MTCL respectively, but in A♂ 73% shorter. ♂ do not acquire significantly longer outer rectrices with age, I♂ only 4% shorter than A♂, but gain a progressively grossly longer central pair. MLL of A♀ 11% shorter than in A♂, but as a proportion of MWL similar in both sexes. MBL of A♀ 4% shorter, but as a proportion of MWL 3% longer. MFPL  $216 \pm 53\text{mm}$  ( $n = 59$ ).

Central rectrices of SA♂ show immense variation, as in *P. raggiana*.

Four allopatric subspecies have been widely accepted (Mayr, 1941; Gilliard 1969). Mean measurements are so similar overall for the subspecies *minor*, *pulchra* and *finschi* as to be of little diagnostic use. Variation in plumage and colouration is far more helpful.

1) *P. m. minor* Shaw, 1809. General Zoology - Aves, 7, pt. 2, p. 486 'New Guinea', restricted to Dorey, Vogelkop. Now known from west New Guinea eastward in the north to Humboldt Bay and in the south to Etna Bay. MFPL of A♂  $215 \pm 60\text{mm}$  ( $n = 23$ ).

2) *P. m. finschi* Meyer, 1885. Zeitschrift für die gesamte Ornithologie 2, 383. Karan, between Aitape and the mouth of the Sepik, at longitude  $142^{\circ}30'\text{E}$ . Now known from northern New Guinea from the Aitape region and Sepik Valley eastward

to Astrolabe Bay and the Upper Ramu R. Yellow shoulder marking less extensive than in other subspecies. On average similarly sized to nominate but flank plumes brighter orange-yellow and MFPL slightly shorter ( $203 \pm 40\text{mm}$ ,  $n = 25$ ).

3) *P. m. jobiensis* Rothschild, 1897. Bulletin of the British Ornithologists' Club 6, 46. Jobi I (= Yapen I). Only known from Yapen I. Generally larger than nominate, MWL, MTL and MLL of A♂ 6, 8 & 8% longer respectively. Flank plume colour as nominate and MFPL slightly longer ( $250 \pm 55\text{mm}$ ,  $n = 11$ ).

4) *P. m. pulchra* Mayr & de Schauensee, 1939. Proceedings of the Academy of Natural Sciences of Philadelphia 91: 151. Tip, Misool I. Only known from Misool I. Like nominate but brown of plumage said to be more purplish, less reddish (Gilliard, 1969). MWL, MTL and MLL of A♂ very slightly larger than nominate, but samples too small for meaningful comparisons, and there is considerable overlap in all size ranges between the two forms.

The availability of 11 specimens from Misool I allowed Mees (1965) to re-assess the validity of *P. m. pulchra*, originally described from only two birds (Mayr & de Schauensee, 1939). Mees concluded that Misool I birds did not differ consistently from birds of the adjacent mainland (*P. m. minor*). LeCroy (1981) subsequently presented measurements suggesting that, while Misool I birds are a little larger than adjacent mainland birds, there is considerable overlap. Our measurements show far less difference in size between the two forms, birds of Misool I being no larger than those of the Vogelkop and certainly not even close to 'large as in *jobiensis*' (Gilliard, 1969). In any event it appears that this subspecies should be synonymised with *minor*.

#### **Paradisaea decora** Goldie's Bird of Paradise (Table 39)

*Paradisaea decora* Salvin & Godman, 1883. Ibis 1883, p. 131. Fergusson I. Only known from D'Entrecasteaux Archipelago (Fergusson and Normanby Is). Monotypic. A♀ slightly smaller than A♂, MWL by 11%, but only one A♂ MW known. MTL of A♀ also shorter (7%) than A♂, but as a proportion of MWL 4% longer. MTL of A♀ and I♂ 17 & 15% longer than MTCL respectively, but in A♂ they are 68% shorter. ♂ do not acquire longer outer rectrices with age, those of I♂ similar to A♂, but gain a progressively grossly longer central pair. MLL of A♀ 10% shorter than in A♂ but as a proportion of MWL similar in both



sexes. MBL of A ♀ negligibly (2%) shorter but as a proportion of MWL negligibly (2%) longer. MFPL of A ♂  $203 \pm 42\text{mm}$  ( $n = 14$ ).

Central tail rectrices of SA ♂ show great variation, as in *P. raggiana*.

***Paradisaea rubra* Red Bird of Paradise**  
(Table 40)

*Paradisaea rubra* Daudin, 1800. *Traité d'Ornithologie* (Lesson). 2: 271. 'New Guinea' in error for Waigeu I. Monotypic. A ♀ slightly smaller than A ♂, MWL and MW by 10 & 21% respectively. MTL of A ♀ also shorter (4%) than A ♂, but as a proportion of MWL 4% longer. MTL similar to MTCL in I ♂, but 8% longer in A ♀ and 79% shorter in A ♂. ♂ do not acquire longer outer rectrices with age, I ♂ as A ♂, but gain a progressively grossly longer central pair. MLL of A ♀ 7% shorter than in A ♂, but as a proportion of MWL similar in both sexes. MBL of A ♀ also 3% shorter, but as a proportion of MWL only negligibly (2%) longer. MFPL  $94 \pm 15\text{mm}$  ( $n = 21$ ).

Central tail rectrices of SA ♂ show immense variation, as in *P. raggiana*.

***Paradisaea guilielmi* Emperor Bird of Paradise** (Table 41)

*Paradisaea guilielmi* Cabanis, 1888. *Journal für Ornithologie* 36: 119. 'Kaiser Wilhelm's Land' (restricted to the Sattelberg, Huon Peninsula, PNG). Monotypic. A ♀ smaller than A ♂, MWL by 11% smaller, but no weights available for comparisons. MTL of A ♀ also shorter (7%) than in A ♂, but as a proportion of MWL slightly (3%) longer. MTL of A ♀ and I ♂ very slightly (2 & 3%) longer than MTCL respectively, but in A ♂ 80% shorter. ♂ acquire a progressively grossly longer central pair with slightly shorter (3%) outer rectrices but our samples of I ♂ too small for meaningful comparisons. MLL of A ♀ 9% shorter than in A ♂, but as a proportion of MWL similar in both sexes. MBL of A ♀ negligibly (2%) shorter, but as a proportion of MWL slightly (2%) longer. MFPL of A ♂  $77 \pm 38\text{mm}$  ( $n = 20$ ).

***Paradisaea rudolphi* Blue Bird of Paradise**  
(Table 42)

A ♀ smaller than A ♂, MWL and MW by 5 & 13% respectively. MTL of A ♀ 13% longer than in A ♂ and as a proportion of MWL 10% longer. MTL of A ♀ and I ♂ similar to MTCL, unlike congeners, but in A ♂ 80% shorter. ♂ acquire shorter outer tail rectrices with age, I ♂ 16%

longer than A ♂, while simultaneously gaining a progressively longer central pair, contrary to congeners, with the possible exception of *P. guilielmi*. MLL and MBL of A ♀ 4 & 2% shorter than in A ♂, but as a proportion of MWL similar in both sexes. MFPL  $88 \pm 16\text{mm}$  ( $n = 26$ ).

Central rectrices of SA ♂ show great variation, as in *P. raggiana*.

Three subspecies are recognised. Mean measurements are so similar overall as to be of little diagnostic use and samples for two subspecies (*ampla* and *margaritae*) are small. Variation in plumage markings and colouration are more helpful.

1) *P. r. rudolphi* (Finsch, 1885). *Zeitschrift für die gesammte Ornithologie* 2: 385, pl. 20. Hufeisengebirge, south-east New Guinea. MFPL of A ♂  $84 \pm 13\text{mm}$  ( $n = 17$ ).

2) *P. r. ampla* Greenway, 1934. *Proceedings of the New England Zoological Club* 14: 1. Mt Missim, Morobe district. Similar to nominate but head lighter, more brownish, less blackish in A ♂ (Gilliard, 1969). Some measurements of *ampla* are on average only slightly smaller than nominate but with much overlap. MFPL of A ♂  $90 \pm 25\text{mm}$  ( $n = 3$ ). In view of comments by Gilliard (1969), Cooper & Forshaw (1977) and Cracraft (1992) regarding the questionable validity of *P. r. ampla*, it seems that merging this subspecies into nominate *P. r. rudolphi* is overdue.

3) *P. r. margaritae* Mayr & Gilliard, 1951. *American Museum Novitates* 1524: 11. Kimil R, 20 miles west-northwest of Nondugl, Wahgi Valley, Central Highlands, Mandated Territory of New Guinea. Like nominate but ♀ with underparts uniformly and narrowly barred blackish. MTL and MLL of A ♂ and A ♀ on average shorter than in the nominate, but samples too small for meaningful conclusions. MFPL  $101 \pm 10.3\text{mm}$  ( $n = 4$ ). Only one or two birds of the Tari Valley area have been collected, and it is not known to which subspecies they should be allocated. We did not examine them.

**PARADISAEA SPECIES.** We found our figures for the various *Paradisaea* taxa in close agreement with those of Lecroy (1981), considering the often gross differences in sample sizes. We cannot compare our 'total bill length' with 'exposed bill length' (see Methods). Small differences in measuring techniques between ourselves and Lecroy (1981) are reflected by negligibly to slightly longer tail lengths and slightly (2–5mm) larger tarsus measurements than ours. In calculating the MTL as a proportion of MWL, these differences might, therefore, become significant.

Differences between LeCroy's measurements of 'unplumed males' and ours for 'immature males' suggest that the former may have included males with signs of A ♂ plumage, other than flank plumes. Our 'immature males' class included only ♀-plumed birds showing absolutely no sign of ♂ plumage.

### SYSTEMATIC CONCLUSIONS

The following systematic list includes taxa accepted by the above review. Genera and their sequence are those of Beehler & Finch (1985), with the addition of those taxa extralimital to New Guinea. Species and subspecies, the latter presented chronologically, are those of Gilliard (1969); those marked with an asterisk have been described since Gilliard (1969). Names in parenthesis are those of subspecies included in Gilliard (1969) that were invalid (*L. s. pseudoparotia*) or are not accepted herein. For consistency herein and ease of reference with that work only spelling of genus and specific names are as in Gilliard (1969). It should be noted, however, that a few of these have been subsequently corrected.

#### PARADISAEIDAE

##### CNEMOPHILINAE

###### *Cnemophilus*:

*C. m. macgregorii*, *C. m. (kuboriensis) sanguineus*, *C. l. loruae*, *C. l. anethystina*, *C. l. inexpectata*

###### *Loboparadisaea*:

*L. s. sericea*, *L. s. aurora*

#### PARADISAEINAE

###### *Macgregoria*:

*M. p. pulchra*, *M. p. carolinae*

###### *Lycocorax*:

*L. p. pyrrhopterus*, *L. p. morotensis*, *L. p. obiensis*

###### *Manucodia*:

*M. a. ater*, *M. a. alter*, *M. a. subalter*, *M. chalybata*, *M. c. comrii*, *M. c. trobriandi*, *M. (rubensis) jobiensis*, *M. k. keraudrenii*, *M. k. gouldi*, *M. k. jamesii*, *M. k. hunsteini*, *M. k. (mayeri) purpureoviolaceus*, *M. k. neumanni*, *M. k. adelberti*, *M. k. aruensis*\*, *M. k. diamondi*\*

###### *Paraligalla*:

*P. (intermedia) carunculata*, *P. brevicauda*

###### *Ptiloris*:

*P. paradiseus*, *P. victoriae*, *P. m. magnificus*, *P. m. intercedens*, *P. m. alberti*

###### *Semioptera*:

*S. w. wallacei*, *S. w. halmaherae*

###### *Selencudis*:

*S. m. melanoleuca*, *S. m. auripennis*

###### *Epimachus*:

*E. a. (geisleri, inversus) albertisi*, *E. a. cervinicauda*, *E. bruijnii*, *E. f. fasmosus*, *E. f. (stresemanni) atratus*, *E. f. ultimus*\*, *E. m. meyeri*, *E. m. (megarhynchus) albicans*, *E. m. bloodi*

###### *Astrapia*:

*A. nigra*, *A. s. splendidissima*, *A. s. (elliottsmithi) helios*, *A. mayeri*, *A. s. stephaniae*, *A. s. (ducalis) feminina*, *A. rothschildi*

###### *Lophorina*:

*L. s. superba*, *L. s. niedda*, *L. s. (sphinx) minor*, (*L. s. pseudoparotia*), *L. s. (connectens, addenda) latipennis*, *L. s. feminina*

###### *Parotia*:

*P. wahnesi*, *P. sefilata*, *P. c. carolae*, *P. c. berlepschi*, *P. c. meeki*, *P. c. chulcothorax*, *P. c. chrysenia*, *P. c. clelandiae*, *P. l. (fuscior, exhibita) lawesii*, *P. l. helenae*

###### *Preridophora*:

*P. (burgersi, hallstromi) alberti*

###### *Cicimurus*:

*C. r. (rex, gymnorrhynchus) regius*, *C. r. (similis, cryptorrhynchus) coccineifrons*, *C. m. magnificus*, *C. m. (intermedius) chrysopterus*, *C. m. hunsteini*, *C. respublica*

###### *Paradisaea*:

*P. r. raggiana*, *P. r. augustaevictoriae*, *P. r. intermedia*, (*P. r. granti*), *P. r. salvadori*, *P. a. apicala*, *P. a. novaequeguinea*, *P. m. (pulchra) minor*, *P. m. finschi*, *P. m. jobiensis*, *P. decora*, *P. rubra*, *P. guillelmi*, *P. r. (ampla) rudolphi*, *P. r. margaritae*

### ACKNOWLEDGEMENTS

For much appreciated permission to access and help with the study of ornithological collections in their care we sincerely thank the following persons and institutions: Steve Van Dyck, Glen Ingram and Carden Wallace, Queensland Museum, Brisbane; Richard Schodde, Ian Mason and John Wombey, Australian National Wildlife Collection, CSIRO, Canberra; Walter Boles and Wayne Longmore, Australian Museum, Sydney; Les Christidis and Rory O'Brien, Museum of Victoria, Melbourne; Philippa Horton, South Australian Museum, Adelaide; Glen Storr and Ron Johnstone, Western Australian Museum, Perth; Barry Baker, Belinda Dettmann, Australian Bird and Bat Banding Scheme, Canberra; Dean Amadon, Chris Blake, Walter Bock, Joel Cracraft, Mary LeCroy, Manny Levine and Lester Short, American Museum of Natural History, New York; Robert Prys-Jones, Michael Walters and Peter Coulston, Ornithology, The Natural History Museum, London; Ned Johnson, Museum of Vertebrate Zoology, University of Cali-

ifornia, Berkeley; David Willard, The Field Museum, Chicago; Raymond A. Paynter Jr., Museum of Comparative Zoology, Cambridge; Allen Allison and Carla Kishinami, Bishop Museum, Honolulu; James Dick and Brad Millen, Royal Ontario Museum, Toronto; Frank Gill, Academy of Natural Sciences, Philadelphia; James M. Loughlin, The Carnegie Museum of Natural History, Pittsburgh; Fred C. Sibley, Peabody Museum, Yale University, New Haven; Gene K. Hess, Delaware Museum of Natural History, Wilmington; Mohammad Amir and Darjono, Museum Zoologicum Bogoriense, Bogor; Frank Bonaccorso, Iliaiah Bigilale and Paul Wanga, National Museum and Art Gallery of Papua New Guinea, Port Moresby; Clem Fisher, National Museums & Galleries, Liverpool; Josefina Barreiro, Museo Nacional de Ciencias Naturales, Madrid; Giuliano Doria, Museo Civico, Genova; Rene Dekker and Peter Van Dam, Nationaal Natuurhistorisch Museum, Leiden; Per Ericson, Gunnar Johansson and Göran Frisk, Swedish Museum of Natural History, Stockholm; Jon Fjeldså, Zoologisk Museum Københavns Universitet, København; Eric Pasquet, Museum National d'Histoire Naturelle, Paris; Siegfried Eck, Staatliches Museum für Tierkunde, Dresden; Josef H. Reichholf, Ornithology, Zoologische Staatssammlung, München; Burkhard Stephan, Zoologisch Museum, Berlin; R. van den Elzen, Museum Alexander Koenig, Bonn, for kindly forwarding skins to Frankfurt. Claus König, Staatliches Museum für Naturkunde, Stuttgart, for kind hospitality in addition to access to collections; D. Stefan Peters, Joachim Steinbacher, Martina Küsters and Karin Böhm, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt; H. Hoerschelmann, Zoologisches Institut und Zoologisches Museum, Hamburg.

People who kindly provided hospitality, interest and help in other ways include Joan Airey, Marion Buchanan, Brian and Del Coates, Jeff and Barbara Davies, Paul and Luisa Frith, Peter and Daphne Fullagar, Andrew and Trish Gillison and Peter and Janet Marsack. Sincere thanks to the Chapman Fund and the Fund Committee for the support enabling us to examine the remarkable and fine collections of the American Museum of Natural History. We sincerely thank Walter Boles and Ralph E. Molnar for helpful constructive comment and editorial work.

Dedicated to the memory of Charles Walter De Vis (Rev.), (1829-1915), Curator at the Queensland Museum, who described several birds of paradise.

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## APPENDIX 1

TABLE 1. Measurements (mm) and weights (g) of specimens of *Cnemophilus macgregorii*

	Wing length	Tail length	Tarsus length	Total head length	Bill length	Bill width	Weight
<i>C. m. macgregorii</i>							
<b>Males: adult</b>							
Mean	113	92	40.8	54.9	29.1	5.7	98
SD	2.26	2.48	1.82	1.49	1.55	0.37	4.51
Min	107	86	37.8	53.2	24.1	4.9	94
Max	117	96	45.8	59.1	32.0	6.5	104
n	22	22	23	17	24	21	4
<b>subadult</b>							
Mean	112	92	40.8	54.4	30.4	5.8	
SD	3.00	2.99	1.77	1.05	0.44	0.49	
Min	107	88	39.3	53.3	29.7	5.3	
Max	115	95	43.1	55.4	30.7	6.4	
n	5	4	5	3	4	4	
<b>immature</b>							
Mean	111	94	40.7	53.2	29.8	5.5	81
SD	2.94	4.30	0.67	1.15	1.33	0.36	
Min	107	91	39.8	51.9	27.9	5.0	
Max	116	103	41.8	54.1	31.3	5.9	
n	7	7	7	3	6	7	1
<b>Females: adult</b>							
Mean	108	93	39.3	52.1	27.1	5.6	91
SD	3.44	4.37	2.25	0.91	1.41	0.44	
Min	104	89	35.7	50.9	25.0	5.0	
Max	114	101	42.6	53.3	29.4	6.3	
n	10	9	9	7	10	10	1
<i>C. m. sanguineus</i>							
<b>Males: adult</b>							
Mean	115	91	41.2	52.8	28.3	5.7	105
SD	2.43	2.58	1.46	0.25	1.13	0.47	11.56
Min	110	86	38.0	52.6	25.8	4.8	94
Max	118	96	44.3	53.1	30.0	6.4	120
n	26	25	26	3	22	24	5
<b>subadult</b>							
Mean	115	89	42.0	53.3	29.1	5.9	86
SD	2.35	3.76	1.95	0.14	0.89	0.35	
Min	112	84	39.3	53.2	27.7	5.3	
Max	118	94	43.8	53.4	30.1	6.3	
n	6	6	6	2	6	6	1
<b>immature</b>							
Mean	114	90	41.6	52.7	27.7	5.6	87
SD	2.56	2.79	1.40	0.99	1.11	0.47	

Min	108	87	38.9	52	26.0	5.0	
Max	119	97	43.3	53.4	29.7	6.6	
n	16	15	16	2	16	16	1
<b>Females: adult</b>							
Mean	111	89	40.2	49.8	26.0	5.61	93
SD	3.61	3.77	1.54	0.07	1.49	0.33	13.02
Min	101	80	37.6	49.7	23.0	4.8	79
Max	115	97	42.7	49.8	28.0	6.4	125
n	22	22	22	2	21	22	9

<i>C. m. kuroboriensis</i>							
<b>Males: adult</b>							
Mean	112	88	41.6		29.6	5.3	94
SD	0.96	0.96	0.92		1.36	0.26	
Min	111	87	40.6		28.0	5.0	
Max	113	89	42.7		30.9	5.6	
n	4	4	4		4	4	1
<b>immature</b>							
Mean	112	87	39.5		27.2	5.6	97
n	1	1	1		1	1	1
<b>Females: adult</b>							
Mean	109	83	39.0		25.6	5.2	
SD	2.83	2.83	0.49		0.00	0.14	
Min	107	81	38.6		25.6	5.1	
Max	111	85	39.3		25.6	5.3	
n	2	2	2		2	2	

<b>all subspecies</b>							
<b>Males: adult</b>							
Mean	114	91	41.1	54.7	28.8	5.7	100
SD	2.59	2.67	1.62	1.64	1.40	0.43	9.37
Min	107	86	37.8	52.6	24.1	4.8	90
Max	118	96	45.8	59.1	32.0	6.5	120
n	53	52	54	21	51	50	11
<b>subadult</b>							
Mean	113	90	41.4	54.0	29.6	5.8	86
SD	2.84	3.66	1.88	0.96	0.95	0.39	
Min	107	84	38.3	53.2	27.7	5.3	
Max	118	95	43.8	55.4	30.7	6.4	
n	11	10	11	5	10	10	1
<b>immature</b>							
Mean	113	91	41.2	53.0	28.2	5.6	88
SD	2.90	3.79	1.29	0.99	1.48	0.42	8.08
Min	107	87	38.9	51.9	26.0	5.0	81
Max	119	103	43.3	54.1	31.3	6.6	97
n	24	23	24	5	23	24	3
<b>Females: adult</b>							
Mean	110	90	39.9	51.6	26.3	5.6	93
SD	3.68	4.50	1.74	1.30	1.49	0.36	11.77
Min	101	80	35.7	49.7	23.0	4.8	79
Max	115	101	42.7	53.3	29.4	6.4	125
n	34	33	33	9	33	34	11

TABLE 2. Measurements (mm) and weights (g) of specimens of *Cnemophilus loriae*

	Wing length	Tail length	Tarsus length	Total head length	Bill length	Bill width	Weight
<i>C. l. loriae</i>							
<b>Males: adult</b>							
Mean	103	75	37.3	53.3	26.6	6.5	83
SD	2.15	2.55	1.60	1.39	1.37	0.37	7.41
Min	99	71	34.3	51.1	21.4	5.6	76
Max	107	81	42	55.5	29.4	7.4	94
n	29	29	28	15	29	28	7
<b>subadult</b>							
Mean	100	74	36		25.8	6.4	
n	1	1	1		1	1	
<b>immature</b>							
Mean	102	77	37.0	51.2	25.8	6.2	89
SD	1.20	2.93	1.25	0.71	1.48	0.22	9.85
Min	101	71	35.2	50.5	22.4	6	81
Max	104	81	38.3	52.1	27.2	6.6	100
n	9	9	9	4	9	9	3
<b>Females: adult</b>							
Mean	102	77	36.6	51.5	26.1	6.4	86
SD	2.39	3.71	1.56	0.97	0.82	0.40	6.21
Min	98	72	34.2	49.6	24.3	5.7	78
Max	106	84	40.4	53.4	27.5	7.1	96
n	18	18	18	12	18	18	8
<i>C. l. amethystina</i>							
<b>Males: adult</b>							
Mean	105	77	37.0	52.5	26.1	6.3	93
SD	2.14	2.08	1.49	1.13	0.65	0.34	8.95
Min	101	73	32.3	50.7	24.7	5.6	80
Max	109	81	39.1	53.8	27.5	6.8	101
n	25	25	25	7	25	25	5
<b>subadult</b>							
Mean	106	80	37.2	53.3	26.5	6.3	98
SD	1.98	3.11	0.89	1.87	0.84	0.36	
Min	102	75	35.9	51.3	24.9	5.7	
Max	108	85	38.7	55	27.9	6.9	
n	12	13	13	3	13	13	1
<b>immature</b>							
Mean	103	80	36.9	53.2	26.4	6.5	82
SD	2.52	2.73	1.11	0.57	0.69	0.43	14.61
Min	100	75	34.8	52.5	24.9	5.7	66
Max	107	86	38.9	54.1	27.6	7.3	100
n	14	14	14	7	13	14	6
<b>Females: adult</b>							
Mean	103	80	36.9	51.5	25.9	6.3	78.6
SD	2.94	3.67	1.49	1.37	0.76	0.35	11.18
Min	98	73	34	49.6	24.3	6	69
Max	109	88	39.9	53.8	27.2	7.2	95
n	20	20	20	7	19	20	7
<i>C. l. inexpectata</i>							
<b>Males: adult</b>							
Mean	103	71	37.5	52.6	26.4	6.2	79
SD	2.72	2.61	1.40	0.97	0.93	0.31	4.35
Min	97	66	34.7	51.1	25.2	5.5	75
Max	107	77	40.0	53.8	28.7	6.7	85
n	25	25	24	6	24	24	4
<b>subadult</b>							
Mean	103	71	37.3	52.9	26.2	6.4	
SD	2.66	2.78	0.97	0.00	0.81	0.23	
Min	99	66	36.4	52.9	25.3	6	
Max	107	76	38.9	52.9	27.6	6.8	
n	8	8	8	3	8	8	
<b>immature</b>							
Mean	104	76	38.3	53.0	27.0	6.1	87
SD	3.04	3.25	0.73	0.95	0.93	0.47	

Min	100	70	36.9	52.2	25.1	5.2	
Max	109	81	39.2	54.6	28.3	7	
n	13	13	12	5	13	13	1
<b>Females: adult</b>							
Mean	102	73	36.4	51.3	26.0	6.3	80
SD	2.34	2.63	1.17	0.92	0.92	0.42	10.47
Min	97	69	34.4	49.7	24.0	5.1	60
Max	108	79	38.6	52.5	28.0	7.2	95
n	27	28	28	10	28	28	8

<b>all subspecies</b>							
<b>Males: adult</b>							
Mean	104	74	37.3	53.0	26.4	6.3	85
SD	2.44	3.53	1.50	1.27	1.05	0.37	9.08
Min	97	66	32.3	50.7	21.4	5.5	75
Max	109	81	42	55.5	29.4	7.4	101
n	79	79	77	28	78	77	16
<b>subadult</b>							
Mean	104	76	37.2	53.1	26.4	6.3	98
SD	2.64	5.39	0.91	1.20	0.81	0.31	
Min	99	66	35.9	51.3	24.9	5.7	
Max	108	85	38.9	55.0	27.9	6.9	
n	21	22	22	6	22	22	1
<b>immature</b>							
Mean	103	78	37.4	52.6	26.5	6.3	85
SD	2.53	3.48	1.21	1.09	1.10	0.42	12.27
Min	100	70	34.8	50.5	22.4	5.2	66
Max	109	86	39.2	54.6	28.3	7.3	100
n	36	36	35	16	35	36	10
<b>Females: adult</b>							
Mean	103	76	36.6	51.4	26.0	6.3	81
SD	2.56	4.40	1.37	1.03	0.84	0.39	9.55
Min	97	69	34	49.6	24.0	5.1	60
Max	109	88.1	40.4	53.8	28.0	7.2	96
n	65	66	66	29	65	66	23

TABLE 3. Measurements (mm) and weights (g) of specimens of *Loboparadisea sericea*

	Wing length	Tail length	Tarsus length	Total head length	Bill length	Bill width	Weight
<i>L. s. sericea</i>							
<b>Males: adult</b>							
Mean	94	55	31.1	44.6	20.4	6.1	72
SD	2.32	2.42	1.08	1.00	1.04	0.56	0.21
Min	90	52	28.8	43.2	18.8	5.2	72
Max	98	59	33.5	46.5	23.0	7.2	72
n	17	16	16	9	16	15	2
<b>immature</b>							
Mean	97	60	31.8	43.6	20.4	6.3	62.7
SD	1.15	4.32	0.83		0.70	0.19	
Min	96	56	30.7		19.8	6	
Max	98	66	32.7		21.4	6.4	
n	3	4	4	1	4	4	1
<b>Females: adult</b>							
Mean	98	58	31.9	47.2	21.4	7.1	
SD	1.83	2.71	0.83	0.07	0.58	0.49	
Min	96	55	31	47.1	20.8	6.5	
Max	101	63	33.3	47.2	22.2	7.6	
n	6	6	6	2	6	4	
<b>immature</b>							
Mean	97	60	31.4	45.7	20.5	6.5	76
SD	2.27	1.96	0.79	0.46	0.46	0.30	1.56
Min	92	56	30.4	45.4	19.7	6.1	75
Max	99	63	32.6	46.2	21.4	6.9	77
n	10	10	10	3	9	9	2

*L. s. aurora*

<b>Males: adult</b>							
Mean	97	59	31.3	45.5	21.2	6.5	62
SD	1.91	1.45	0.91	1.08	1.01	0.40	8.87
Min	93	56	29.4	43.2	19.8	5.8	50
Max	100	61	32.6	47.2	24.2	7.3	75
n	16	16	16	11	16	14	12
<b>immature</b>							
Mean	96	63	30.6	46.1	21.4	6.2	70
SD	0.71	1.63	2.19	0.28	0.28	0.07	5.20
Min	95	62	29.0	45.9	21.2	6.1	63
Max	96	64	32.1	46.3	21.6	6.2	75
n	2	2	2	2	2	2	4
<b>Females: adult</b>							
Mean	97	63	30.9	47.0	22.7	6.6	73
SD	5.13	0.61	1.51	0.55	0.60	0.21	2.83
Min	91	62	29.8	46.5	22.1	6.4	71
Max	101	63	32.6	47.6	23.3	6.8	75
n	3	3	3	3	3	3	2
<b>immature</b>							
Mean	99	63	31.8	46.2	21.3	7.2	70
SD	3.24	3.37	0.88	1.44	0.53	0.28	8.81
Min	93	59	30.3	43.6	20.2	6.7	60
Max	102	69	32.8	47.8	21.6	7.6	77
n	7	7	7	6	7	7	3

## all subspecies

<b>Males: adult</b>							
Mean	95	57	31.2	45.1	20.8	6.3	64
SD	2.68	2.74	0.98	1.11	1.09	0.51	8.94
Min	90	52	28.8	43.2	18.8	5.2	50
Max	100	61	33.5	47.2	24.2	7.3	75
n	33	32	32	20	32	29	14
<b>immature</b>							
Mean	96	61	31.4	45.3	20.7	6.2	68
SD	1.10	3.79	1.34	1.46	0.77	0.16	5.43
Min	95	56	29.0	43.6	19.8	6.0	63
Max	98	66	32.7	46.3	21.6	6.4	75
n	5	6	6	3	6	6	5
<b>Females: adult</b>							
Mean	97	59	31.5	47.1	21.8	6.9	73
SD	3.00	3.26	1.11	0.40	0.85	0.43	2.83
Min	91	55	29.8	46.5	20.8	6.4	71
Max	101	63	33.3	47.6	23.3	7.6	75
n	9	9	9	5	9	7	2
<b>immature</b>							
Mean	98	61	31.6	46.0	20.9	6.8	72
SD	2.94	3.23	0.82	1.19	0.60	0.44	7.10
Min	92	56	30.3	43.6	19.7	6.1	60
Max	102	69	32.8	47.8	21.6	7.6	77
n	17	17	17	9	16	16	5

TABLE 4. Measurements (mm) and weights (g) of specimens of *Macgregoria pulchra*

	Wing length	Tail length	Tarsus length	Total head length	Bill length	Bill width	Weight
<i>M. p. pulchra</i>							
<b>Males: adult</b>							
Mean	202	161	61.3	70.0	39.4	6.1	256
SD	5.78	3.15	2.24	2.65	1.57	0.26	13.37
Min	187	156	54.6	65.8	36.9	5.5	242
Max	211	168	64.6	74.5	42.4	6.5	274
n	19	18	19	10	18	18	6
<b>Females: adult</b>							
Mean	183	147	56.1	68.5	37.8	5.9	198
SD	4.35	3.06	0.92	2.22	0.29	0.29	8.62
Min	175	143	55.1	65.0	35.0	5.6	190
Max	187	152	57.7	71.7	41.7	6.4	207
n	7	7	6	1	7	7	3
<i>M. p. caroliniae</i>							
<b>Males: adult</b>							
Mean	192	134	64.4	73.7	41.6	6.0	349
SD	5.27	3.95	1.27	2.05	2.14	0.23	12.02
Min	184	128	62.0	70.8	37.3	5.4	340
Max	200	141	65.9	76.5	44.0	6.1	357
n	10	10	10	5	10	8	2
<b>Females: adult</b>							
Mean	172	124	58.3	68.2	37.8	5.6	230
SD	4.13	4.63	2.78	1.18	1.67	0.29	
Min	164	120	52.9	66.3	35.6	5	
Max	179	133	61.3	69.3	40.3	6	
n	10	10	10	5	10	10	1
all subspecies							
<b>Males: adult</b>							
Mean	199	151	62.4	71.2	40.2	6.1	279
SD	7.28	13.61	2.46	3.01	2.06	0.26	44.52
Min	184	128	54.6	65.8	36.9	5.4	242
Max	211	168	65.9	76.5	44.0	6.5	357
n	29	28	29	15	28	26	8
<b>Females: adult</b>							
Mean	177	134	57.4	68.2	37.8	5.7	206
SD	7.18	12.27	2.47	1.07	1.85	0.34	17.63
Min	164	120	52.9	66.3	35.0	5.0	190
Max	187	152	61.3	69.3	41.7	6.4	230
n	17	17	16	6	17	17	4



TABLE 5. Measurements (mm) and weights (g) of specimens of *Lycocorax pyrrhopterus*

	Wing length	Tail length	Tarsus length	Total head length	Bill length	Bill width	Weight
<i>L. p. pyrrhopterus</i>							
Males: adult							
Mean	190	143	42.0	77.6	46.6	11.4	269
SD	8.66	8.41	1.21	0.64	1.65	0.74	22.05
Min	175	127	38.7	76.9	41.8	9.6	242
Max	206	160	44.0	78.3	49.1	13.2	304
n	28	28	27	5	27	28	6
Females: adult							
Mean	186	139	41.7	75.6	44.6	10.9	250
SD	5.76	5.89	1.47	1.72	1.93	0.74	19.22
Min	176	131	38.9	73.1	40.8	9.4	218
Max	197	153	44.7	77.2	48.8	12.0	276
n	27	27	27	7	27	27	7
<i>L. p. moralesensis</i>							
Males: adult							
Mean	219	156	49.2		55.5	12.48	
SD	3.87	4.36	0.99		0.73	0.97	
Min	214	152	48.1		54.5	11.4	
Max	223	161	50.5		56.2	13.3	
n	4	4	4		4	4	
Females: adult							
Mean	209	145	46.5		52.9	11.6	
SD	0.68	2.00	2.23		0.58	0.15	
Min	209	143	44.8		52.6	11.4	
Max	210	147	49		53.6	11.7	
n	3	3	3		3	3	
<i>L. p. obiensis</i>							
Males: adult							
Mean	204	145	45.5	81.9	52.3	12.09	332
SD	7.59	5.49	1.57	2.37	2.51	0.61	25.54
Min	190	135	43.0	78.5	49.0	11	300
Max	224	156	49.3	86.7	56.2	13	370
n	26	26	26	13	26	26	9
Females: adult							
Mean	198	141	45.1	79.6	50.3	11.8	291
SD	5.91	6.36	1.71	1.51	2.14	0.62	27.47
Min	186	130	42.2	77.7	44.9	10.4	250
Max	208	152	47.7	82.0	54.4	12.6	316
n	19	19	19	6	19	19	5
all subspecies							
Males: adult							
Mean	198	145	44.1	80.7	49.8	11.79	302
SD	27.94	19.19	5.45	17.60	6.53	5.53	84.99
Min	175	127	38.7	76.9	41.8	9.6	242
Max	224	161	50.5	86.7	56.2	13.3	370
n	58	58	57	18	57	58	17
Females: adult							
Mean	192	140	43.3	77.5	47.3	11.3	267
SD	9.25	6.09	2.41	2.61	3.67	0.80	30.58
Min	176	130	38.9	73.1	40.8	9.4	218
Max	210	153	47.0	82.0	54.4	12.6	316
n	49	49	47	13	49	49	12

TABLE 6. Measurements (mm) and weights (g) of specimens of *Mamucodia atra*

	Wing length	Tail length	Tarsus length	Total head length	Bill length	Bill width	Weight
<i>M. a. atra</i>							
Males: adult							
Mean	181	150	38.4	68.0	38.9	8.9	224
SD	9.99	10.98	1.89	2.74	2.35	0.65	30.82
Min	160	133	34.5	61.5	34.3	7.8	170
Max	204	170	42.1	72.7	44.6	10.7	315
n	25	25	25	14	25	25	17
immature							
Mean	173	144	38.7	68.9	39.1	9.4	
SD	5.86	10.02	1.61	1.45	2.03	0.58	
Min	164	123	35.1	67.4	36.8	8.3	
Max	185	158	40.8	71.4	42.7	10.5	
n	11	11	11	6	11	11	
Females: adult							
Mean	175	143	38.1	66.4	37.5	8.9	207
SD	9.49	11.59	1.55	2.58	2.03	0.64	27.04
Min	159	127	35.4	62	34.1	7.5	150
Max	196	166	41.4	72.2	42.6	10	244
n	27	27	27	19	27	27	17
immature							
Mean	167	137	36.9	63.4	36.1	8.7	177
SD	7.73	9.40	1.96	1.87	2.43	0.75	29.54
Min	156	125	31.8	61.1	32.7	7.2	144
Max	182	155	39.7	67.1	41.7	10	200
n	17	17	17	9	17	17	5
<i>M. a. alter</i>							
Males: adult							
Mean	204	172	45.2	78.7	46.3	9.6	
SD	3.13	6.16	1.26	1.58	0.37	0.66	
Min	198	163	42.9	76.9	45.8	8.4	
Max	208	182	46.7	80.4	46.8	10.4	
n	7	7	7	5	7	7	
immature							
Mean	195	161	44.4	79.9	44.9	9.8	
n	1	1	1	1	1	1	
Females: adult							
Mean	191	160	42.6	74.8	42.9	9.3	
SD	7.37	7.62	1.08	1.59	0.86	0.59	
Min	182	152	40.9	71.8	40.8	8.6	
Max	201	172	44.2	76.4	44.2	10.3	
n	11	11	11	6	11	11	
<i>M. a. subalter</i>							
Males: adult							
Mean	195	165	41.2	72.5	41.8	9.2	275
SD	8.76	10.55	2.13	2.25	1.59	0.58	26.67
Min	175	144	34.7	67.3	38.6	8.2	203
Max	211	183	44.7	76.5	44.1	10.4	303
n	29	29	28	23	29	29	4
immature							
Mean	184	155	40.4	71.2	39.6	9.2	225
SD	9.18	10.64	1.74	3.84	1.88	0.58	
Min	172	140	37.5	65.8	37.6	8.4	
Max	199	168	42.0	74.9	42.7	10.2	
n	7	7	7	5	7	7	1
Females: adult							
Mean	185	154	39.7	68.9	39.1	9.0	212
SD	8.42	7.94	1.52	1.95	1.22	0.80	13.37
Min	173	138	36.6	65.1	36.9	7.2	140
Max	205	168	43.3	72.9	41.1	10.2	230
n	26	26	26	20	25	26	5

## immature

Mean	188	160	41.6	71.1	39.9	9.7
SD	8.41	5.99	1.00	2.80	1.96	0.33
Min	177	153	40.3	67.2	36.9	9.3
Max	200	168	42.8	75.5	43.0	10.1
n	6	6	6	6	6	6

## all subspecies

<b>Males: adult</b>							
Mean	190	160	40.5	71.7	41.2	9.1	238
SD	12.04	13.11	2.89	4.04	2.96	0.64	36.88
Min	160	133	34.5	61.5	34.3	7.8	170
Max	211	183	46.7	80.4	46.8	10.7	315
n	61	61	60	42	61	61	23
<b>immature</b>							
Mean	178	149	39.7	70.8	39.6	9.4	225
SD	9.65	11.52	2.11	4.00	2.27	0.57	
Min	164	123	36.1	65.8	36.8	8.3	
Max	199	168	44.4	79.9	44.9	10.5	
n	19	19	19	12	19	19	1
<b>Females: adult</b>							
Mean	182	151	39.5	68.6	39.1	9.0	208
SD	10.41	11.62	2.14	3.47	2.48	0.71	21.92
Min	159	127	35.4	62.0	34.1	7.2	155
Max	205	172	44.2	76.4	44.2	10.3	252
n	64	64	64	45	63	64	24
<b>immature</b>							
Mean	172	143	38.1	66.5	37.1	8.9	177
SD	11.95	13.39	2.74	4.46	2.83	0.79	23.54
Min	156	125	31.8	61.1	32.7	7.2	153
Max	200	168	42.8	75.5	43.0	10.1	200
n	23	23	23	15	23	23	3

TABLE 7. Measurements (mm) and weights (g) of specimens of *Manucodia chalybata*

	Wing length	Tail length	Tarsus length	Total head length	Bill length	Bi. width	Weight
<b>Males: adult</b>							
Mean	173	141	37.8	70.1	40.4	9.1	223
SD	5.42	7.03	1.46	2.30	1.75	0.53	24.84
Min	161	128	34.0	64.5	37.6	8.0	164
Max	183	152	41.1	75.7	44.4	10.0	264
n	37	37	34	25	36	37	14
<b>immature</b>							
Mean	169	133	38.3	70.0	40.2	8.9	209
SD	5.68	6.02	1.46	2.46	2.38	0.66	14.44
Min	157	120	34.9	67.4	33.9	7.7	138
Max	179	144	41.9	75.2	44.1	10.2	211
n	21	21	21	10	23	23	12
<b>Females: adult</b>							
Mean	167	136	37.1	66.2	38.3	8.7	209
SD	6.62	7.41	1.45	1.75	1.86	0.56	17.80
Min	153	124	34.6	61.8	34.4	7.7	160
Max	182	154	41.6	68.3	42.5	9.4	264
n	27	27	27	15	26	27	12
<b>immature</b>							
Mean	161	130	37.5	66.0	37.0	8.7	172
SD	5.34	5.74	1.53	2.75	2.04	0.47	13.46
Min	150	114	36.0	60.2	34.0	8.0	144
Max	175	144	40.9	71	41.8	9.5	200
n	12	12	12	11	21	21	3

TABLE 8. Measurements (mm) and weights (g) of specimens of *Manucodia cornii*

	Wing length	Tail length	Tarsus length	Total head length	Bill length	Bi. width	Weight
<b>Males: adult</b>							
Mean	244	173	50.8	90.3	57.6	11.5	448
SD	6.58	5.74	1.22	1.83	1.86	0.59	
Min	229	162	48.4	85.8	53.2	10.4	
Max	257	182	52.7	93.9	61.0	12.7	
n	23	22	23	19	23	23	1
<b>immature</b>							
Mean	233	164	50.5		51.8	11.5	
n	1	1	1		1	1	
<b>Females: adult</b>							
Mean	231	165	49.3	85.0	53.2	11.1	418
SD	4.99	3.94	1.71	2.51	1.79	0.60	
Min	223	158	46.3	82.0	50.8	10.2	
Max	240	170	51.4	90.1	56.9	12.3	
n	13	13	13	10	13	13	1
<b>immature</b>							
Mean	219	163	48.3	83.8	51.4	11.2	
SD	7.09	8.41	0.72	2.40	2.24	0.24	
Min	207	149	47.2	82.1	49.6	10.9	
Max	224	171	49.0	85.5	54.7	11.5	
n	5	5	5	2	5	5	
<b>Males: adult</b>							
Mean	226	158	49.5	85.5	54.8	11.1	
SD	7.32	6.31	1.33	2.84	1.81	0.64	
Min	213	148	46.7	80.6	51.6	10.1	
Max	235	169	51.6	88.0	56.5	12.3	
n	14	14	14	7	14	14	
<b>Females: adult</b>							
Mean	217	154	48.4	83.7	52.8	10.8	
SD	4.59	7.60	1.77	2.35	2.36	0.35	
Min	209	147	46.3	81.2	49.9	10.2	
Max	223	172	52.0	87.8	57.1	11.2	
n	9	9	9	6	9	9	
<b>immature</b>							
Mean	204	149	45.4	80.4	49.7	9.9	
n	1	1	1	1	1	1	
<b>all subspecies</b>							
Mean	237	167	50.3	89.1	56.6	11.4	448
SD	11.19	9.66	1.39	3.01	2.31	0.64	
Min	213	148	46.7	80.6	51.6	10.1	
Max	257	182	52.7	93.9	61.0	12.7	
n	37	36	37	26	37	37	1
<b>immature</b>							
Mean	233	164	50.5		51.8	11.5	
n	1	1	1		1	1	
<b>Females: adult</b>							
Mean	225	160	48.9	84.5	53.1	11.0	418
SD	8.63	7.92	1.75	2.65	2.00	0.54	
Min	209	147	46.3	81.2	49.9	10.2	
Max	240	172	52.0	90.1	57.1	12.3	
n	22	22	22	16	22	22	1
<b>immature</b>							
Mean	217	160	47.8	82.7	51.1	11.0	
SD	8.93	9.35	1.35	2.60	2.12	0.56	
Min	204	149	45.4	80.4	49.6	9.9	
Max	224	171	49.0	85.5	54.7	11.5	
n	6	6	6	3	6	6	

TABLE 9. Measurements (mm) and weights (g) of specimens of *Manuodiodia jobiensis*

	Wing length	Tail length	Tarsus length	Total head length	Bill length	Bill width	Weight
<i>M. j. jobiensis</i>							
Males: adult							
Mean	184	140	37.6	73.9	40.6	9.7	245
SD	6.13	6.16	1.31		0.39	0.73	16.97
Min	178	132	36.1		40	8.9	233
Max	192	147	39.3		40.9	10.6	257
n	4	4	4	1	4	4	2
Females: adult							
Mean	174	130	36.8	65.7	37.2	9.1	205
SD	1.41	2.83	0.64	0.07	0.71	0.57	
Min	173	128	36.3	65.6	36.7	8.7	
Max	175	132	37.2	65.7	37.7	9.5	
n	2	2	2	2	2	2	1
<i>M. j. rubiensis</i>							
Males: adult							
Mean	175	132	37.1	68.5	38.7	9.2	222
SD	6.64	7.04	1.76	2.91	2.26	0.70	8.23
Min	161	119	34	63.1	34.6	7.6	212
Max	194	146	40.5	73.4	42.4	10.5	232
n	26	25	25	21	26	26	6
immature							
Mean	170	128	36.6	66.4	38.4	9.0	197
SD	3.10	4.24	0.78	1.03	1.25	0.62	
Min	167	123	35.6	65.5	37.4	8.3	
Max	174	132	37.3	67.5	39.8	9.8	
n	4	4	4	3	3	4	1
Females: adult							
Mean	168	127	36.1	65.6	37.0	9.2	174
SD	4.94	6.37	1.23	2.56	1.34	0.66	24.96
Min	157	113	33.5	61.2	34.6	7.8	150
Max	177	141	39.2	69.5	39.1	10.1	200
n	24	24	24	19	24	24	4
immature							
Mean	166	119	35.3	62.2	35.5	8.8	
SD	4.24	2.12	0.14	3.18	1.48	0.49	
Min	159	120	35.2	59.9	34.4	8.4	
Max	169	120	35.4	64.4	36.5	9.1	
n	2	2	2	2	2	2	
all subspecies							
Males: adult							
Mean	176	133	37.1	68.7	39.0	9.3	228
SD	7.24	7.41	1.70	3.07	2.20	0.71	14.30
Min	161	119	34.0	63.1	34.6	7.6	212
Max	194	147	40.5	73.9	42.4	10.6	257
n	30	29	29	22	30	30	8
immature							
Mean	170	128	36.6	66.4	38.4	9.0	197
SD	3.10	4.24	0.78	1.03	1.25	0.62	
Min	167	123	35.6	65.5	37.4	8.3	
Max	174	132	37.3	67.5	39.8	9.8	
n	4	4	4	3	3	4	1
Females: adult							
Mean	169	127	36.1	65.6	37.0	9.2	180
SD	5.01	6.20	1.20	2.43	1.30	0.64	25.74
Min	157	113	33.5	61.2	34.6	7.8	150
Max	177	141	39.2	69.5	39.1	10.1	205
n	26	26	26	21	26	26	5
immature							
Mean	166	119	35.3	62.2	35.5	8.8	
SD	4.24	2.12	0.14	3.18	1.48	0.49	
Min	163	117	35.2	59.9	34.4	8.4	
Max	169	120	35.4	64.4	36.5	9.1	
n	2	2	2	2	2	2	

TABLE 10. Measurements (mm) and weights (g) of specimens of *Manuodiodia keraudrenii*

	Wing length	Tail length	Tarsus length	Total head length	Bill length	Bill width	Weight
<i>M. k. keraudrenii</i>							
Males: adult							
Mean	160	124	34.0	62.5	33.5	8.0	149
SD	4.84	5.47	1.55	1.54	1.31	0.70	14.06
Min	144	110	30.2	60.1	31.1	6.6	130
Max	166	133	37.0	64.7	36.3	9.8	175
n	24	24	24	16	24	24	7
immature							
Mean	155	125	34.8	62.7	33.2	7.7	
SD	6.06	2.45	1.21	0.59	0.91	0.40	
Min	148	122	32.9	61.8	32.1	6.9	
Max	165	129	36.7	63.1	35.0	8.2	
n	8	8	8	4	8	8	
Females: adult							
Mean	152	117	32.9	59.8	31.6	7.7	136
SD	5.16	5.46	1.02	1.52	1.62	0.45	4.76
Min	139	108	31.2	57.5	28.8	7.0	130
Max	158	125	34.7	62.1	33.6	8.5	140
n	15	15	15	7	15	15	7
immature							
Mean	145	117	31.3	59.8	32.9	7	126
n	1	1	1	1	1	1	1
<i>M. k. gauldi</i>							
Males: adult							
Mean	165	135	36.8	62.6	33.7	7.0	161
SD	4.64	3.80	1.31	1.47	1.04	0.36	12.81
Min	155	124	33.8	60.3	31.8	6.2	150
Max	177	142	39.2	65.7	35.7	7.7	184
n	35	35	35	17	32	33	6
immature							
Mean	155	137	37.5	63.7	35.2	6.7	
n	1	1	1	1	1	1	
Females: adult							
Mean	158	127	35.0	60.1	31.7	7.1	138
SD	3.79	2.33	1.15	1.58	1.04	0.47	
Min	151	122	32.8	56.6	30.1	6.3	
Max	166	130	37.7	61.6	33.8	8.2	
n	16	16	15	8	16	16	1
immature							
Mean	147	124	33.66	59.1	31.9	6.8	
SD	5.13	2.30	1.42	1.80	1.08	0.74	
Min	142	122	31.5	57.3	30.5	6.0	
Max	154	127	35.5	60.9	33.2	7.6	
n	5	5	5	3	5	5	
<i>M. k. jamesii</i>							
Males: adult							
Mean	164	128	35.8	64.1	34.3	8.2	187
SD	4.32	4.67	1.49	2.65	1.71	0.58	4.45
Min	155	119	32.5	57.1	29.7	7.4	183
Max	171	138	37.7	68.2	36.4	9.8	190
n	26	26	26	14	26	26	2
immature							
Mean	143	114	37.3	59.5	31.9	6.9	175
SD							0.71
Min							174
Max							175
n	1	1	1	1	1	1	2
Females: adult							
Mean	160	125	35.6	61.7	33.3	7.9	160
SD	5.23	5.34	1.88	1.42	1.62	0.54	17.66
Min	148	119	31.8	60.2	31.0	7.3	147
Max	166	135	38.7	63.6	37.1	9.3	172
n	13	13	13	4	13	13	2

## immature

Mean	151	123	34.0	61.4	32.6	7.5
SD	6.15	3.46	1.32	1.81	1.45	0.63
Min	142	118	32.0	58.7	31.0	6.6
Max	159	128	35.9	63.8	35.7	8.5
n	9	9	9	8	9	9

*M. k. hunsteini*

<b>Males: adult</b>						
Mean	188	139	39.2	67.3	36.6	8.5
SD	3.71	3.07	0.81	1.07	0.80	0.59
Min	179	133	37.1	65.8	35.2	7.7
Max	194	143	40.6	68.6	37.6	9.7
n	13	13	13	8	13	13

## immature

Mean	176	133	40.0	66.0	35.9	8.2
SD	4.04	0.58	0.49	0.14	0.50	0.57
Min	174	133	39.7	65.9	35.4	7.7
Max	181	134	40.6	66.1	36.4	8.8
n	3	3	3	2	3	3

## Females: adult

Mean	182	135	37.9	62.9	34.8	8.3
SD	2.60	3.64	1.62	1.67	1.22	0.36
Min	179	132	35.0	61.4	32.5	7.9
Max	186	141	39.7	64.7	36.8	8.9
n	8	8	8	3	8	8

## immature

Mean	172	131	37.5	62.6	33.7	8.4
SD	2.94	4.19	1.46	0.85	0.66	0.58
Min	169	127	36.3	61.7	32.9	7.7
Max	175	137	39.5	63.4	34.3	9.1
n	4	4	4	3	4	4

*M. k. purpleviolaceus*

<b>Males: adult</b>						
Mean	168	127	37.0	66.0	35.4	8.0
SD	3.94	5.04	1.14	1.72	1.54	0.51
Min	157	115	34.4	61.5	31.0	7.0
Max	174	138	38.8	68.9	38.4	9.3
n	35	35	35	26	34	35

## immature

Mean	166	126	37.8	64.7	35.3	7.6
SD	6.24	1.71	0.73	0.49	0.83	0.37
Min	159	124	37.2	64.3	34.4	7.1
Max	174	128	38.6	65	36.4	8
n	4	4	4	2	4	4

## Females: adult

Mean	162	123	35.8	63.3	33.6	7.6
SD	6.28	4.71	1.65	1.57	1.07	0.35
Min	148	113	31.5	60.3	31.6	6.7
Max	180	133	38.2	67.1	36.5	8.2
n	29	29	29	21	29	29

## immature

Mean	157	125	35.4	62.7	33.1	7.9
SD	3.79	1.15	1.76	1.53	1.12	0.95
Min	154	124	34.3	61.5	32.3	7.0
Max	161	126	37.4	64.4	34.4	8.9
n	3	3	3	3	3	3

*M. k. neumanni*

<b>Males: adult</b>						
Mean	156	124	33.1	61.7	32.9	7.7
SD	3.53	3.51	0.69	2.79	1.82	0.37
Min	150	119	32.0	58.7	30.2	7.0
Max	162	129	34.3	65.8	36.4	8.2
n	11	11	11	6	10	11

## immature

Mean	145	117	33.9	60	31.8	8.2
SD	4.24	4.24	0.78	0.28	0.28	0.07
Min	142	114	33.3	59.8	31.6	8.1
Max	148	120	34.4	60.2	32.0	8.2
n	2	2	2	2	2	2

## Females: adult

Mean	149	117	33.2	58.9	31	7.9
SD	3.21	4.59	1.92	0.62	0.51	0.42
Min	142	110	30.0	58.2	30.4	7.3
Max	152	123	34.8	59.7	32.1	8.6
n	8	8	8	4	8	8

*M. k. mayri*

<b>Males: adult</b>						
Mean	169	132	36.7	66.4	35.9	7.8
SD	3.65	4.07	0.96	0.92	0.61	0.23
Min	164	128	35.0	65.0	34.9	7.4
Max	175	138	38.2	67.3	36.8	8.1
n	7	6	7	5	6	7

## immature

Mean	160	125	36.5	62.2	32.3	7.4
n	1	1	1	1	1	1

## Females: adult

Mean	160	126	36.0	63.5	33.3	7.5
SD	6.38	6.16	1.53	0.72	0.77	0.33
Min	151	120	34.3	62.7	32.4	7.1
Max	166	135	38.2	64.5	34.3	7.9
n	5	5	5	5	5	5

## immature

Mean	155	124	35.4	61.7	32.3	7.4
SD	5.51	5.13	0.10	1.73	1.81	0.58
Min	151	118	35.3	60.2	31.0	7.1
Max	161	128	35.5	63.6	34.4	8.1
n	3	3	3	3	3	3

*M. k. adelberth*

<b>Males: adult</b>						
Mean	163	130	33.9		33.0	7.9
SD	3.89	5.42	2.76		1.21	0.62
Min	156	122	27.8		30.8	7.1
Max	168	139	37.0		34.8	9.2
n	10	10	9		9	10

## Females: adult

Mean	157	126	32.5		32.1	7.5
n	1	1	1		1	1

## immature

Mean	146	121	34.45	55.1	30.85	7.45
SD	0	1.41	0.64		2.19	0.21
Min	146	120	34.0		29.3	7.3
Max	146	122	34.9		32.4	7.6
n	2	2	2	1	2	2

*M. k. aruensis*

<b>Males: adult</b>						
Mean	168	136	35.5	63.5	33.6	7.6
SD	2.06	2.63	1.73	0.57	0.44	0.37
Min	166	132	34.2	63.1	33.0	7.3
Max	170	138	38.0	63.9	33.9	8.1
n	4	4	4	2	4	4

## immature

Mean	158	134	37.2	62.4	33.2	8.0
SD	4.00	7.02	0.66	1.30	0.82	0.49
Min	154	127	36.6	61.1	32.5	7.4
Max	162	141	37.9	63.7	34.1	8.3
n	3	3	3	3	3	3

*M. k. diamondi*

<b>Males: adult</b>						
Mean	171	129	37.4	65.2	35.6	7.8
SD	5.82	4.87	1.70	0.85	1.48	0.51
Min	156	121	34.2	63.7	33.4	7.3
Max	176	134	40.0	65.9	38.0	9.0
n	11	11	9	6	11	11

<b>immature</b>							
Mean	164	127	37.7		34.1	6.8	174
n	1	1	1		1	1	1
<b>Females: adult</b>							
Mean	162	123	35.2	60.6	32.7	7.4	172
SD	3.83	1.50	2.06	2.19	1.67	0.67	0.71
Min	159	121	32.2	58.2	30.9	6.7	171
Max	167	124	36.7	62.5	34.8	8.3	172
n	4	4	4	3	4	4	2
<b>immature</b>							
Mean	172	128	36.2		33.6	7.7	
n	1	1	1		1	1	

<b>all subspecies</b>							
<b>Males: adult</b>							
Mean	167	130	36.1	64.4	34.4	7.8	171
SD	8.32	6.39	2.10	2.48	1.72	0.67	19.79
Min	144	110	27.8	57.1	29.7	6.2	130
Max	194	143	40.6	68.9	38.4	9.8	240
n	176	175	173	100	169	174	49
<b>immature</b>							
Mean	159	127	36.6	62.8	33.8	7.7	168
SD	10.09	6.41	2.07	2.01	1.49	0.54	18.31
Min	142	114	32.9	59.5	31.6	6.7	136
Max	181	141	40.6	66.1	36.4	8.8	182
n	24	24	24	16	24	24	5
<b>Females: adult</b>							
Mean	160	124	35.1	61.8	32.8	7.6	151
SD	9.23	6.53	2.06	2.19	1.63	0.53	14.77
Min	139	108	30.0	56.6	28.8	6.3	130
Max	186	141	39.7	67.1	37.1	9.3	182
n	97	99	98	55	99	99	36
<b>immature</b>							
Mean	155	125	34.8	61.1	32.6	7.5	141
SD	9.92	4.39	1.84	2.26	1.40	0.74	16.08
Min	142	117	31.3	55.1	29.3	6.0	126
Max	175	137	39.5	64.4	35.7	9.1	163
n	28	28	28	22	28	28	5

TABLE 11. Measurements (mm) and weights (g) of specimens of *Paradigalla carunculata*

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<b>Males: adult</b>								
Mean	186	132	160	49.0		43.1	5.3	
SD	6.06	4.33	10.61	0.77		2.41	1.48	
Min	180	122	132	47.9		38.0	4.2	
Max	201	147	170	50.2		47.0	6.7	
n	10	10	10	9		8	9	
<b>immature</b>								
Mean	171	124	133	47.9	69.6	43.7	5.7	
SD	7.25	7.41	9.29	2.24	0.71	2.72	0.37	
Min	160	116	121	44.4	69.1	42.4	5.2	
Max	179	130	148	49.8	70.1	44.1	6.4	
n	7	7	7	7	2	7	7	
<b>Females: adult</b>								
Mean	165	125	132	45.6	67.9	42.2	6.0	170
SD	6.66	7.13	4.71	2.92		2.57	1.41	
Min	157	118	125	41.4		37.1	5.2	
Max	175	131	138	50.2		44.0	6.4	
n	11	9	9	11	1	10	9	

TABLE 12. Measurements (mm) and weights (g) of specimens of *Paradigalla brevicauda*

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<b>Males: adult</b>								
Mean	158	53	51	44.0	71.6	44.2	5.6	173
SD	3.84	9.62	7.63	1.06	0.78	1.65	0.41	12.12
Min	151	44	42	41.5	69.4	39.6	4.9	160
Max	168	88	73	45.6	74.4	48.9	6.2	184
n	25	25	24	25	8	23	25	3
<b>immature</b>								
Mean	159	78	78	43.2	69.6	44.0	5.8	169
SD	3.66	15.04	14.60	1.59	2.38	2.12	0.32	6.86
Min	148	54	53	39.8	67.1	40.1	5.2	160
Max	164	107	106	46.3	73.8	48.0	6.6	175
n	30	29	26	30	14	27	30	4
<b>Females: adult</b>								
Mean	150	68	67	41.9	70.9	44.4	5.9	163
SD	2.96	15.50	12.78	1.10	1.42	1.49	0.35	10.61
Min	144	45.7	53	39.1	67.3	42.1	5.2	156
Max	154	96	91	43.9	72.3	47.9	6.5	170
n	26	26	23	26	12	25	25	2
<b>immature</b>								
Mean	153	89	78	42.4	70	44.7	6.3	
SD	0.71	5.66	15.56	0.85		0.78		
Min	152	85	67	41.8		44.1		
Max	153	93	89	43.0		45.2		
n	2	2	2	2	1	2	2	

TABLE 13. Measurements (mm) and weights (g) of specimens of *Ptiloris paradiseus*

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<b>Males: adult</b>								
Mean	160	98	89	33.3	80.1	54.1	6.4	141
SD	2.75	2.11	2.20	1.34	2.19	2.48	0.42	11.65
Min	153	92	84	30.1	75.0	49.3	5.6	131
Max	165	103	95	36.2	84.4	61.6	7.2	152
n	37	37	37	35	21	34	36	5
<b>subadult</b>								
Mean	154	96	94	33.9	80.3	54.1	6.5	
SD	2.14	1.70	1.62	0.97	1.50	1.13	0.34	
Min	151	94	91	31.9	77.5	52.7	5.8	
Max	158	100	97	35.2	81.8	56.7	6.9	
n	13	12	12	13	7	12	13	
<b>immature</b>								
Mean	148	94	91	32.9	80.5	54.5	6.0	114
SD	6.35	3.77	2.65	1.19	3.58	3.48	0.33	1.59
Min	139	89	88	31.4	77.3	51.9	5.5	111
Max	154	98	93	34.5	85.3	60.6	6.4	115
n	5	4	3	5	4	5	5	2
<b>Females: adult</b>								
Mean	144	91	87	32.3	82.9	58.5	6.1	104
SD	5.07	3.45	3.37	1.41	2.23	2.97	0.38	2.27
Min	137	86	83	29.5	76.5	51.1	5.2	89
Max	156	99	96	35.6	85.8	65.8	7.0	112
n	26	26	23	24	15	25	26	7

TABLE 14. Measurements (mm) and weights (g) of specimens of *Ptiloris victorinae*

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<b>Males: adult</b>								
Mean	139	81	77	32.1	68.6	43.2	6.0	105
SD	3.06	1.75	2.11	1.00	1.32	1.24	0.35	7.13
Min	133	77	72	29.8	65.5	40.1	5.3	91
Max	146	85	81	34.6	71.7	46.7	6.9	119
n	51	51	51	51	40	51	51	22
<b>subadult</b>								
Mean	134	83	81	32.4	67.4	42.9	6.0	105
SD	3.63	1.77	2.11	1.01	1.33	1.83	0.34	
Min	125	81	79	30.7	65.5	40.0	5.5	
Max	138	86	86	34.2	69.4	45.7	6.5	
n	11	10	9	11	7	11	11	1
<b>immature</b>								
Mean	129	81	79	32.3	67.4	42.7	5.9	93
SD	3.91	2.29	2.00	1.39	0.85	1.35	0.35	5.31
Min	121	75	74	29.7	66.2	40.3	5.3	82
Max	134	85	83	34.5	68.6	45.8	6.5	104
n	25	23	20	24	11	24	25	22
<b>Females: adult</b>								
Mean	125	78	76	30.3	68.9	44.7	5.9	86
SD	5.00	3.59	2.84	1.55	1.85	2.22	0.30	5.87
Min	116	72	72	28.0	64.2	40.1	5.4	77
Max	136	85	83	33.1	72.3	49	6.5	96
n	34	33	31	31	27	33	32	25

TABLE 15. Measurements (mm) and weights (g) of specimens of *Ptiloris magnificus*

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<b>Males: adult</b>								
Mean	192	102	97	39.6	88.4	59.7	6.9	207
SD	4.54	4.07	4.54	1.09	2.06	2.37	0.49	13.61
Min	182	92	88	37.2	84.7	54.2	5.8	180
Max	200	110	108	42.3	91.2	63.5	8.0	230
n	31	31	29	29	10	31	31	20
<b>subadult</b>								
Mean	186	109	108	40.1	86.1	59.7	7.3	182
SD	7.22	2.83	5.82	1.13	3.68	3.00	0.56	
Min	177	105	97	37.9	83.5	56	6.3	
Max	196	114	116	41.5	88.7	65.5	7.8	
n	9	9	7	9	2	9	8	1
<b>immature</b>								
Mean	177	109	110	39.9	89.9	58.9	7.2	180
SD	4.07	3.78	2.77	1.14	1.36	2.63	0.38	8.28
Min	169	102	105	36.9	88.2	50.6	6.6	168
Max	183	118	117	41.2	91.7	62.6	9.2	190
n	20	20	18	20	6	20	20	9
<b>Females: adult</b>								
Mean	157	99	99	35.5	80.8	52.6	7.0	142
SD	5.22	4.80	5.41	0.90	2.15	2.78	0.38	19.58
Min	147	91	90	33.1	77.6	44.6	6.2	120
Max	165	113	115	36.9	83.8	56.9	7.9	185
n	25	25	25	24	8	25	25	8

<i>P. m. alberti</i>								
<b>Males: adult</b>								
Mean	181	99	91	37.9	82.3	55.0	6.0	160
SD	3.19	2.33	3.14	1.01	1.38	1.51	0.29	12.04
Min	174	94	83	35.6	79.5	50.9	5.6	143
Max	187	106	98	40.1	85	57.3	6.8	171
n	40	38	35	39	19	34	38	4
<b>subadult</b>								
Mean	171	102	102	37.8	81.1	54.7	5.9	137
SD	5.75	5.01	5.25	1.33	3.91	1.55	0.53	
Min	160	94	92	35.1	71.9	50.5	5.3	
Max	182	111	107	39.5	83.7	56.3	7.5	
n	14	14	8	14	8	14	14	1
<b>immature</b>								
Mean	161	101	102	38.3	80.5	54.1	6.0	131
SD	7.12	3.11	2.61	0.80	3.19	1.74	0.29	
Min	151	97	98	37.6	76.1	50.8	5.6	
Max	169	104	105	39.3	83.3	56	6.3	
n	6	5	5	5	4	6	5	1
<b>Females: adult</b>								
Mean	149	96	93	35.1	76.6	50.6	5.8	104
SD	7.64	6.10	5.65	3.06	3.77	2.96	0.25	9.07
Min	139	88	86.4	31.1	71.8	45.8	5.4	94
Max	165	108	107	44.2	82.4	55.7	6.3	112
n	24	21	16	24	18	23	24	3

<i>P. m. intercedens</i>								
<b>Males: adult</b>								
Mean	193	101	96	40.4	84.1	55.8	7.0	184
SD	3.03	2.92	3.73	1.44	2.04	2.01	0.39	15.20
Min	188	96	90	36.8	80.4	52.4	6.2	155
Max	199	106	105	42.7	88.1	61.9	7.7	214
n	25	25	25	23	17	24	25	12
<b>subadult</b>								
Mean	191	109	102	40.1	85.1	55.0	7.2	166
SD	4.36	2.03	5.22	1.48	1.14	1.51	0.40	42.85
Min	185	107	98	38.2	83.8	52.0	6.5	120
Max	197	113	109	42.4	86.6	57.2	7.8	211
n	9	9	5	9	6	9	9	3
<b>immature</b>								
Mean	175	108	106	40.5	83.2	54.8	7.1	176
SD	5.94	4.02	3.91	1.11	1.33	1.53	0.54	9.49
Min	162	103	100	38.4	81.5	51.3	5.7	165
Max	187	116	113	42.5	87	57.5	8.2	189
n	20	20	19	19	17	19	20	7
<b>Females: adult</b>								
Mean	152	98	97	35.2	75.0	48.0	6.8	126
SD	4.46	3.26	3.06	1.21	1.54	1.31	0.34	13.10
Min	145	92	91	32.6	72.0	45.3	6.3	102
Max	162	103	105	38.1	77.5	50.7	7.6	147
n	27	27	23	27	20	27	27	15

all subspecies								
<b>Males: adult</b>								
Mean	188	101	95	39.1	84.3	56.8	6.6	194
SD	7.13	3.39	4.66	1.57	2.93	2.89	0.63	21.38
Min	174	92	83	35.6	79.5	50.9	5.6	143
Max	200	110	108	42.7	91.2	63.5	8.0	230
n	96	94	89	91	46	89	94	36
<b>subadult</b>								
Mean	181	106	104	39.1	83.2	56.2	6.7	163
SD	10.68	4.94	5.89	1.72	3.65	3.01	0.84	34.32
Min	160	94	92	35.1	71.9	50.5	5.3	120
Max	197	114	116	42.4	88.7	65.5	7.8	205
n	32	32	20	32	16	32	31	5
<b>immature</b>								
Mean	174	107	107	40.0	84.3	56.5	7.0	175
SD	7.27	4.37	4.18	1.27	3.57	2.98	0.56	14.21
Min	161	97	98	36.9	76.1	50.6	5.6	131
Max	187	118	117	42.5	91.7	62.6	8.2	190
n	46	45	42	44	27	45	45	17
<b>Females: adult</b>								
Mean	153	98	97	35.3	76.6	50.3	6.6	128
SD	6.67	4.86	5.31	1.92	3.37	3.08	0.62	18.67
Min	139	88	86.4	31.1	71.8	44.6	5.4	94
Max	165	113	115	44.2	83.8	56.9	7.9	185
n	76	73	64	75	46	75	76	26

TABLE 16. Measurements (mm) and weights (g) of specimens of  
*Semioptera wallacei*

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<i>S. w. wallacei</i>								
<b>Males: adult</b>								
Mean	156	78	66	41.9	73.0	45.1	6.6	163
SD	2.56	4.61	4.17	1.08	1.37	1.63	0.39	11.02
Min	152	71	60	39.4	70.6	41.2	5.7	152
Max	162	90	81	44.3	74.7	47.5	7.3	174
n	29	28	27	28	14	26	25	3
<b>subadult</b>								
Mean	156	85	79	42.2	71.4	45.5	6.7	
SD	2.43	3.27	9.03	0.64	1.84	0.60	0.34	
Min	153	79	66	41.1	70.1	44.8	6.3	
Max	159	87	87	42.9	72.7	46.4	7.2	
n	6	6	6	6	2	5	5	
<b>Immature</b>								
Mean	150	87	88	41.3	72.0	44.9	6.7	153
SD	4.62	1.58	2.00	2.18	1.52	0.98	0.44	3.54
Min	141	85	84	35.9	70.2	43.6	6.2	150
Max	156	89	90	43.5	74.1	47.2	7.7	155
n	11	11	11	11	7	11	11	2
<b>Females: adult</b>								
Mean	145	84	85	39.9	70.7	43.8	6.7	135
SD	4.45	3.49	4.04	1.49	0.95	1.02	0.42	8.54
Min	135	78	76	37.1	69.1	41.5	6.0	126
Max	154	94	96	43.3	72.2	46.5	7.7	143
n	26	25	24	25	17	24	25	3
<i>S. w. halmaherae</i>								
<b>Males: adult</b>								
Mean	157	85	74	41.7	72.2	44.2	6.7	
SD	2.64	3.40	5.27	1.20	1.36	1.79	0.38	
Min	153	79	67	39.0	70.3	39.9	6.1	
Max	162	93	93	43.9	74.0	47.8	7.6	
n	32	31	30	30	9	31	30	
<b>subadult</b>								
Mean	154	86	82	41.9	71.0	43.6	6.5	
SD	4.04	1.92	6.98	0.55	2.91	2.67	0.46	
Min	149	84	74	41.4	67.8	41.5	5.9	
Max	160	89	90	42.6	73.5	48.2	6.9	
n	5	5	5	5	3	5	5	
<b>Immature</b>								
Mean	154	90	91	41.5	70.1	43.9	7.2	
SD	2.92	3.18	3.28	0.95	1.04	1.68	0.39	
Min	147	84	86	39.5	68.8	42.3	6.6	
Max	157	94	96	42.5	71.3	47.1	7.4	
n	8	8	8	8	4	7	8	
<b>Females: adult</b>								
Mean	144	86	87	38.6	70.0	43	6.9	
SD	3.30	2.30	2.57	1.00	1.46	1.46	0.42	
Min	138	81	84	36.2	68.0	40.6	6.1	
Max	151	90	91	40.3	72.0	45.7	7.5	
n	25	25	21	25	13	24	25	
<b>all subspecies</b>								
<b>Males: adult</b>								
Mean	157	82	70	41.8	72.7	44.6	6.7	163
SD	2.62	5.36	6.55	1.14	1.38	1.76	0.39	11.02
Min	152	71	60	39.0	70.3	39.9	5.7	152
Max	162	93	93	44.3	74.7	47.8	7.6	174
n	61	59	57	58	23	57	55	3
<b>subadult</b>								
Mean	155	85	80	42.1	71.2	44.6	6.6	
SD	3.23	2.76	7.98	0.59	2.27	2.06	0.40	
Min	149	79	66	41.1	67.8	41.5	5.9	
Max	160	89	90	42.9	73.5	48.2	7.2	
n	11	11	11	11	5	10	10	

## immature

Mean	152	88	89	41.4	71.3	44.5	6.9	153
SD	4.27	2.76	2.96	1.73	1.62	1.35	0.49	3.54
Min	141	84	84	35.9	68.8	42.3	6.2	150
Max	157	94	96	43.5	74.1	47.2	7.8	155
n	19	19	19	19	11	18	19	2
<b>Females</b>								
Mean	144	85	86	39.3	70.4	43.3	6.8	135
SD	3.91	3.04	3.58	1.40	1.22	1.33	0.42	8.54
Min	135	78	76	36.2	68.0	40.6	6.0	126
Max	154	94	96	43.3	72.2	46.5	7.7	143
n	51	50	45	50	30	48	50	3

TABLE 17. Measurements (mm) and weights (g) of specimens of  
*Seleucidis melanoleuca*

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<i>S. m. melanoleuca</i>								
<b>Males: adult</b>								
Mean	177	71	70	41.0	102.0	71.0	7.4	205
SD	4.27	4.22	3.54	2.19	2.33	2.22	0.6	11.15
Min	167	62	63	30.6	95.4	65.2	6.0	190
Max	185	86	78	43.5	105.9	74.8	8.3	217
n	34	34	33	33	18	32	34	4
<b>subadult</b>								
Mean	179	97	100	41.1	100.1	70.5	7.5	196
SD	5.32	8.27	9.58	1.03	2.28	1.80	0.63	
Min	169	81	78	38.0	95.0	64.9	6.3	
Max	187	112	112	43.0	102.9	73.1	8.7	
n	22	22	20	22	9	22	22	1
<b>Immature</b>								
Mean	177	110	108	41.4	100.3	70.1	7.8	202
SD	4.58	4.16	4.73	1.30	2.40	2.52	0.67	19.1
Min	163	102	101	37.7	96.3	63.6	6.4	182
Max	184	120	121	43.3	103.9	73.1	8.8	220
n	22	21	21	22	8	22	22	3
<b>Females: adult</b>								
Mean	165	108	108	38.0	92.8	64.5	7.5	187
SD	3.17	3.22	4.00	0.81	2.82	2.53	0.68	1.41
Min	158	102	101	36.6	84.3	56.7	6.4	186
Max	171	113	115	39.9	96.7	68.6	8.9	188
n	21	19	19	20	16	21	20	2
<i>S. m. aeneipennis</i>								
<b>Males: adult</b>								
Mean	168	65	66	39.3	95.5	65.3	6.8	189
SD	2.39	2.64	2.15	1.05	2.11	1.80	0.74	10.58
Min	163	61	62	37.0	92.1	62.5	5.7	170
Max	173	70	71	41.9	98.4	68.2	8.4	202
n	25	25	25	25	12	25	25	12
<b>subadult</b>								
Mean	168	93	92	39.6	95.2	66.2	7.0	188
SD	3.59	5.65	8.44	1.08	1.89	2.21	0.68	15.79
Min	164	85	75	37.1	92.8	63.7	6.1	153
Max	179	107	104	41.2	97.7	71.5	8.6	200
n	16	16	15	16	6	16	16	9
<b>Immature</b>								
Mean	166	100	97	39.1	93.7	63.9	6.9	175
SD	2.33	4.24	3.02	0.87	3.19	2.67	0.81	11.88
Min	161	95	92	36.7	89.9	60.0	5.1	158
Max	169	112	103	40.1	98.8	69.0	8.4	188
n	15	15	12	15	8	14	14	5
<b>Females: adult</b>								
Mean	158	99	98	36.5	88.8	60.5	7.1	161
SD	4.46	4.45	5.90	1.51	1.02	2.25	0.60	1.73
Min	152	93	90	34.3	87.0	55.5	6.2	160
Max	169	111	112	39.9	89.8	64.1	8.2	163
n	19	19	18	19	6	18	19	3



all subspecies								
<b>Males: adult</b>								
Mean	173	69	68	40.3	99.4	68.5	7.1	193
SD	5.61	4.55	3.70	1.97	3.92	3.53	0.73	12.57
Min	161	61	62	30.6	92.1	62.5	5.7	170
Max	184	86	78	43.5	105.9	74.8	8.4	217
n	5	59	58	58	30	57	57	10
<b>subadult</b>								
Mean	174	95	97	40.5	98.2	68.7	7.3	189
SD	5.65	7.43	9.95	1.26	3.25	2.89	0.69	15.08
Min	162	81	75	37.1	92.5	63.7	6.1	153
Max	184	112	112	43.0	102.9	73.1	8.7	200
n	2	38	35	38	15	38	38	10
<b>immature</b>								
Mean	173	106	104	40.4	97.0	67.7	7.5	185
SD	5.68	6.56	6.60	1.61	4.37	3.96	0.84	19.71
Min	161	95	92	36.7	89.9	60.0	5.1	158
Max	184	120	121	43.3	103.9	73.1	8.8	220
n	2	36	33	37	16	36	36	8
<b>Females: adult</b>								
Mean	162	103	103	37.3	91.7	62.7	7.3	171
SD	5.61	5.73	6.87	1.42	3.06	3.10	0.66	14.31
Min	151	93	90	34.3	84.3	55.5	6.2	160
Max	181	113	115	39.9	96.7	68.6	8.9	188
n	2	38	37	39	22	37	37	18

TABLE 18 Measurements (mm) and weights (g) of specimens of *Epimachus albertisi*

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<i>E. a. albertisi</i>								
<b>Males: adult</b>								
Mean	155	134	135	34.1	101.0	78.3	5.62	112
SD	2.81	3.66	3.32	0.76	1.72	2.05	0.66	8.29
Min	151	125	129	32.8	97.9	74.7	4.3	106
Max	161	140	141	35.6	103.6	82.6	6.4	126
n	19	19	19	18	8	16	7	6
<b>subadult</b>								
Mean	151	130	133	34.75	102.7	81.2	6.7	
SD	4.95	1.41	2.12	0.64				
Min	147	129	131	34.3				
Max	154	131	134	35.2				
n	2	2	2	2	1	1	1	
<b>immature</b>								
Mean	150	132	133	34.4	101.7	80.0	5.1	111
SD	4.36	5.29	4.36	1.49	3.17	2.86	0.10	7.78
Min	145	126	128	33.3	98.7	77.5	5.0	106
Max	153	136	136	36.1	105	93.1	5.2	116
n	3	3	3	3	2	3	3	2
<b>Females: adult</b>								
Mean	152	130	131	34.8	107.3	84.6	6.1	122
SD	2.49	2.30	2.63	1.23	4.57	4.70	0.25	23.33
Min	150	127	127	33.5	104.4	79.2	5.8	106
Max	156	133	133	36.5	112.6	91.0	6.5	138
n	5	5	4	5	3	5	5	2
<i>E. a. cervinicauda</i>								
<b>Males: adult</b>								
Mean	152	126	125	34.6	97.6	74.9	5.36	112
SD	3.10	3.21	3.60	0.94	2.42	1.99	0.55	6.38
Min	145	121	118	32.2	90.3	69.2	4.3	103
Max	159	131	130	35.7	101.7	79.6	6.5	120
n	2	29	25	28	21	25	2	2

<b>subadult</b>								
Mean	151	124	123	34.38	94.9	74.0	5.9	
SD	0.89	1.44	5.17	0.85	1.09	2.00	0.59	
Min	150	116	116	33.3	94.0	71	5.6	
Max	152	130	130	35.3	95.6	76.7	6.4	
n	5	5	5	5	4	5	5	
<b>immature</b>								
Mean	150	127	129	34.2		76.5	5.2	103
n	1	1	1	1		1	1	
<b>Females: adult</b>								
Mean	147	123	122	33.9	100.3	77.6	6.1	108
SD	2.51	4.47	4.45	0.73	4.18	4.52	1.53	11.44
Min	143	115	115	32.3	91.3	75.1	4.6	99
Max	153	134	132	35.1	106.6	84.7	11	128
n	25	24	21	25	21	24	25	1

<i>E. a. geisleri</i>								
<b>Males: adult</b>								
Mean	152	129	128	35.3		77.2	5.50	
SD	3.54			0.76		1.64		
Min	149			34.7		75.9		
Max	154	134	128	35.8		79.5	6.5	
n	2	1	1	2		2	1	
<b>immature</b>								
Mean	150	130	131	35.7	100.7	75.4	5.8	
SD	5.45	1.55	8.10	1.26	1.00	7.58	2.1	
Min	145	111	120	34.3	97.2	69.4	4.9	
Max	157	135	137	37.2	107.7	85.1	6.6	
n	4	4	4	4	3	4	4	
<b>Females: adult</b>								
Mean	145	122	128	33.9	105.6	82.5	6.2	110
SD	0.58	2.12	4.24	1.15	1.70	3.04	0.32	
Min	145	115	125	32.6	104.4	80.2	5.8	
Max	146	125	131	34.8	106.8	84.7	6.4	
n	3	2	2	3	2	2	2	1

<i>E. a. inversus</i>								
<b>Males: adult</b>								
Mean	159	137		34.0	93.3	71.7	5.10	
n	1	1			1	1	1	
<b>immature</b>								
Mean	153	133	133	34.3	97.5	75.2	5.8	
SD	7.81	0.67	1.15	1.40	0.40	1.13	0.67	
Min	144	127	132	33.2	97.0	74.4	5.0	
Max	158	134	134	35.4	97.5	76	6.1	
n	3	3	3	3	2	2	3	
<b>Females: adult</b>								
Mean	151	125	128	34.2			6.3	
n	1	1	1	1			1	

all subspecies								
<b>Males: adult</b>								
Mean	153	129	129	34.4	98.4	76.1	5.47	112
SD	3.45	5.20	6.09	0.89	2.83	2.62	0.66	6.87
Min	145	121	118	32.2	90.3	69.2	4.3	103
Max	161	140	141	35.8	103.6	82.6	6.5	125
n	51	51	45	49	50	43	46	12
<b>subadult</b>								
Mean	151	126	126	34.49	96.5	75.2	6.0	
SD	2.19	4.10	6.26	0.76	1.65	3.50	0.59	
Min	147	116	116	33.3	94.4	71.1	5.0	
Max	154	131	134	35.3	97.7	81.0	6.7	
n	7	7	7	7	6	6	7	
<b>immature</b>								
Mean	151	131	132	34.8	100.3	76.8	5.5	108
SD	5.22	5.43	5.06	1.33	5.99	5.10	0.60	7
Min	144	119	120	33.2	97.2	69.4	4.6	99
Max	158	134	137	37.2	107.7	85.1	6.6	116
n	11	11	11	11	8	10	11	2
<b>Females: adult</b>								
Mean	148	124	124	34.0	101.5	79.0	6.1	111
SD	2.99	4.58	5.21	0.87	4.74	3.16	1.21	15.41
Min	143	115	115	32.3	97.3	75.1	4.6	99
Max	154	134	133	36.5	112.6	84.7	11	128
n	34	32	28	34	26	31	34	0

TABLE 19. Measurements (mm) and weights (g) of specimens of *Epimachus bruinji*

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<i>E. f. bruinji</i>								
Males: adult								
Mean	160	110	107	33.0	103.2	79.0	6.27	161
SD	3.07	3.29	3.75	0.93	2.64	2.21	0.54	1.89
Min	153	103	100	30.8	98.4	73.5	5.3	160
Max	165	116	115	34.8	107.6	82.6	7.3	164
n	28	26	23	26	17	26	27	4
subadult								
Mean	161	112	109	33.1	103.5	78.4	6.3	165
SD	2.06	3.29	2.87	0.73	0.86	1.62	0.67	6.36
Min	156	104	103	31.7	102.0	74.8	5.6	160
Max	163	115	113	34.1	104.4	80.5	8.1	169
n	18	18	14	18	6	16	16	2
immature								
Mean	157	115	115	32.0	101.0	75.0	7.2	
SD	6.10	4.51	6.59	0.94	2.91	4.77	0.81	
Min	146	109	108	30.4	95.9	62.4	6.0	
Max	164	128	133	33.5	105.4	80.6	8.1	
n	12	12	11	12	8	12	12	
Females: adult								
Mean	155	111	110	32.1	98.1	75.1	6.8	146
SD	4.78	2.91	2.50	1.21	3.19	3.16	0.91	2.65
Min	148	107	107	30.2	93	68.3	5.6	144
Max	162	116	115	33.9	102.4	79.1	8.5	149
n	14	14	12	14	6	12	13	3

TABLE 20. Measurements (mm) and weights (g) of specimens of *Epimachus fastuosus*

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<i>E. f. fastuosus</i>								
Males: adult								
Mean	197	392	710	50.2	105.3	76.5	6.6	266
SD	4.24	37.65	57.05	1.44	2.82	2.06	0.49	1.70
Min	188	340	593	46.5	100.2	72.5	5.9	250
Max	205	539	791	53.5	110.9	80.2	7.6	270
n	24	23	23	23	13	22	23	7
subadult								
Mean	191	274	332	50.67		76.4	6.9	
SD	3.06	20.53	6.11	0.25		1.48	0.23	
Min	188	257	327	50.4		75.1	6.8	
Max	194	297	339	50.9		78	7.2	
n	3	3	3	3		3	3	
immature								
Mean	177	242	304	51.0	103.1	74.5	6.4	222
SD	4.71	10.88	14.52	1.22	5.22	4.97	0.39	1.13
Min	167	226	283	48.8	97.4	67.9	5.7	215
Max	182	257	321	52.5	109.5	81.4	6.8	240
n	8	8	7	8	4	6	8	7
Females: adult								
Mean	166	229	291	47.0	100.1	72.3	6.4	191
SD	10.03	12.48	17.15	2.17	4.23	4.07	0.55	4.74
Min	152	204	270	43.2	95.7	66.4	5.5	174
Max	187	249	321	51.6	104	77.4	7.5	235
n	12	11	12	12	5	10	12	7

*E. f. atratus*

Males: adult								
Mean	199	391	712	50.1	108.0	77.8	6.72	268
SD	7.65	32.23	63.02	1.90	4.34	3.92	0.65	12.04
Min	188	342	640	47.9	102.3	71.4	5.6	255
Max	214	451	856	54.7	114.8	83.8	8.0	280
n	23	21	18	23	14	19	20	5
subadult								
Mean	197	287	461	50.7	109.0	78.6	6.7	250
SD	9.40	42.50	108.19	2.93	5.50	4.26	0.73	
Min	187	254	384	46.7	101.9	73.4	6.0	
Max	208	346	537	53.5	113.8	82.5	7.4	
n	4	4	2	4	4	4	4	1
immature								
Mean	180	250	308	50.4		73.8	6.6	
SD	12.28	6.90	21.88	1.49		6.93	0.65	
Min	164	242	273	48.4		64.8	5.5	
Max	193	255	333	52.3		81.9	7.1	
n	5	5	5	5		5	5	
Females: adult								
Mean	170	215	278	46.8	104.4	76.6	6.8	185
SD	8.45	25.11	31.95	2.63	2.98	2.51	0.58	25.00
Min	154	171	214	42.7	99.5	72.2	5.8	160
Max	187	257	351	53.4	111.2	81.5	8.1	210
n	25	25	17	25	16	25	25	3

*E. f. stresemanni*

Males: adult								
Mean	216	458	847	53.8	113.1	82.6	7.42	315
SD	7.11	39.75	56.63	1.42	2.21	1.92	0.52	2.52
Min	206	421	790	51.0	110.6	80.0	6.6	313
Max	232	537	946	55.4	115.9	85.8	8.2	318
n	12	10	9	12	5	12	12	3
subadult								
Mean	185	365	737	51.6		79.4	6.6	
n	1	1	1	1		1	1	
immature								
Mean	196	267	357	52.2	110.9	80.3	7.8	286
SD	8.43	36.99	51.64	3.18	3.96	2.70	0.52	15.56
Min	179	207	275	45.8	104.7	74.6	6.8	275
Max	205	306	424	56.6	114.6	83.4	8.2	297
n	9	9	8	9	6	9	9	2
Females: adult								
Mean	182	242	322	50.0	109.0	79.4	7.5	237
SD	5.44	15.71	31.87	2.55	1.66	4.51	0.69	26.16
Min	176	230	292	47.3	106.6	71.6	6.0	218
Max	193	280	387	55.0	110.1	88.5	8.3	255
n	11	9	10	11	4	10	11	2

*E. f. ultimus*

Males: adult								
Mean	196	380	725	50.4	101.9	71.7	7.03	278
SD	2.08	7.68	52.08	1.41	0.71	1.36	0.34	3.54
Min	193	374	665	49.1	101.4	69.9	6.6	275
Max	198	391	761	52.4	102.4	73.1	7.3	280
n	4	4	3	4	2	4	4	2
immature								
Mean	183	264	347	50.7	98.3	70.3	6.5	239
SD	5.57	9.93	22.54	1.07	5.94	3.16	0.27	11.51
Min	172	254	320	49.1	94.1	65.7	6.1	223
Max	186	282	382	52.0	102.5	73.7	6.8	252
n	6	6	6	6	2	6	6	6
Females: adult								
Mean	165	235	320	45.6	99.2	70.9	6.5	190
SD	2.63	7.45	15.23	0.84	1.76	1.13	0.37	8.67
Min	161	225	307	44.2	97.0	69.6	6.0	184
Max	168	248	341	46.8	100.7	72.8	7.0	207
n	10	9	8	10	4	10	10	6

all subspecies								
<b>Males: adult</b>								
Mean	201	402	735	50.9	107.4	77.9	6.83	277
SD	9.70	42.82	76.98	2.14	4.42	3.96	0.62	21.11
Min	188	340	593	46.5	100.2	69.9	5.6	250
Max	232	539	946	55.4	115.9	85.8	8.2	318
n	63	58	53	62	34	57	59	17
<b>subadult</b>								
Mean	193	292	443	50.8	109.0	77.9	6.8	250
SD	7.61	42.47	164.66	1.95	5.50	3.16	0.51	
Min	185	254	327	46.7	101.9	73.4	6.0	
Max	208	365	737	53.5	113.8	82.5	7.4	
n	8	8	6	8	4	8	8	1
<b>immature</b>								
Mean	179	256	331	51.2	106.2	75.4	6.9	237
SD	36.67	24.10	39.46	2.11	6.70	5.70	0.76	25.52
Min	0	207	273	45.8	94.1	64.8	5.5	205
Max	205	306	424	56.6	114.6	83.4	8.2	297
n	28	28	26	28	12	26	28	15
<b>Females: adult</b>								
Mean	171	226	298	47.2	103.6	75.3	6.8	195
SD	9.52	21.98	32.05	2.68	4.17	4.28	0.68	24.26
Min	152	171	214	42.7	95.6	66.4	5.5	160
Max	193	280	387	55.0	111.2	88.5	8.3	255
n	58	54	47	58	29	55	58	18

TABLE 21. Measurements (mm) and weights (g) of specimens of *Epimachus meyeri*

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<i>E. m. meyeri</i>								
<b>Males: adult</b>								
Mean	185	261	748	51.1	114.9	84.3	6.7	281
SD	5.96	13.42	56.57	1.56	3.01	3.16	0.50	20.37
Min	177	235	631	48.4	109.8	78.4	5.9	253
Max	206	282	822	54.0	119.9	90.4	7.9	310
n	30	29	23	30	22	25	28	7
<b>subadult</b>								
Mean	182	248	469	51.0	115.96	86.55	7.1	245
SD	5.96	25.73	193.61	0.73	3.62	3.22	0.20	
Min	170	205	308	50.0	112.1	81.4	6.8	
Max	186	276	741	51.9	120.5	88.9	7.3	
n	6	6	4	6	5	6	6	1
<b>immature</b>								
Mean	173	217	335	51.0	112.2	84.0	7.0	236
SD	8.57	21.79	29.84	2.53	6.34	4.08	0.60	33.84
Min	150	180	265	44.8	102.1	76.7	5.8	186
Max	184	260	372	53.9	121.8	91.7	7.9	260
n	19	18	18	19	9	17	17	4
<b>Females: adult</b>								
Mean	163	208	306	46.7	111.2	81.0	6.9	173
SD	11.69	19.41	30.54	3.56	6.84	5.97	0.66	10.47
Min	147	178	257	42.0	95.5	65.6	5.9	162
Max	185	250	359	53.2	120.3	90.5	8.3	188
n	24	24	21	24	16	22	21	6
<i>E. m. albicans</i>								
<b>Males: adult</b>								
Mean	177	247	574	49.5	116.8	85.2	7.02	189
SD	6.57	14.40	71.86	0.79	1.82	2.37	0.76	
Min	171	234	522	48.3	114.8	82.3	6.2	
Max	188	265	656	50.1	118.4	87.2	7.9	
n	5	5	3	4	3	4	5	1

<b>immature</b>								
Mean	168	204	327	47.7	110.7	85.5	6.4	
SD	3.43	20.55	32.18	5.03	4.91	5.14	0.48	
Min	162	171	280	37.9	105.9	77.3	5.8	
Max	171	232	370	51.8	115.7	89.5	7	
n	6	6	5	6	3	5	6	
<b>Females: adult</b>								
Mean	153	193	275	44.9	111.2	83.1	6.3	160
SD	6.78	24.88	39.22	2.10	5.96	5.19	0.52	14.50
Min	142	151	213	39.0	95.6	69.1	5.7	145
Max	170	225	331	47.0	117.2	88.4	7.4	175
n	16	15	9	16	13	15	16	4

<i>E. m. megahynchos</i>								
<b>Males: immature</b>								
Mean	166	229	250	50.7		82.2	6.3	
n	1	1	1	1		1	1	
<b>Females: adult</b>								
Mean	154	221	304	44.2	110.3	80.9	6.8	
SD	0.00	38.89	63.64	0.07		2.55	0.78	
Min	154	193	259	44.1		79.1	6.2	
Max	154	248	349	44.2	110.3	82.7	7.3	
n	2	2	2	2	1	2	2	

<i>E. m. bloodi</i>								
<b>Males: adult</b>								
Mean	177	237	670	48.7	112.9	84.4	6.57	187
SD	2.92	10.58	51.06	1.20	1.43	1.93	0.68	45.69
Min	171	218	595	46.3	110.1	81.7	5.5	144
Max	181	264	766	50.5	114.4	88.5	7.5	230
n	16	16	16	16	8	13	15	6
<b>subadult</b>								
Mean	172	215	437	49.1		86.9	6.4	239
SD	5.20	7.00		2.55		1.21	0.76	5.66
Min	169	210		46.5		85.8	5.6	235
Max	178	223		51.6		88.2	7.1	243
n	3	3	1	3		3	3	2
<b>immature</b>								
Mean	162	219	324	48.0	102.5	79.8	6.4	195
SD	5.73	12.87	13.06	1.57	9.62	6.10	0.49	7.07
Min	151	194	306	45.7	95.7	68.4	5.4	190
Max	169	235	348	49.6	109.3	86.9	7.1	200
n	9	9	7	9	2	8	9	2
<b>Females: adult</b>								
Mean	153	197	288	44.9	108.0	81.8	6.2	163
SD	4.16	12.89	23.22	1.93	3.45	2.49	0.50	27.16
Min	144	171	262	41.3	103.1	78.2	5.3	140
Max	165	226	341	49.8	115.8	88.7	7.3	202
n	23	20	18	23	11	23	23	4

all subspecies								
<b>Males: adult</b>								
Mean	182	252	706	50.2	114.6	84.4	6.68	234
SD	6.69	16.79	75.66	1.78	2.79	2.72	0.59	58.02
Min	171	218	522	46.3	109.8	78.4	5.5	144
Max	206	282	822	54.0	119.9	90.4	7.9	310
n	51	50	42	50	33	42	48	14
<b>subadult</b>								
Mean	178	237	463	50.39	116.0	86.7	6.9	241
SD	7.18	26.42	168.28	1.69	3.62	2.63	0.52	5.29
Min	169	205	308	46.5	112.1	81.4	5.6	235
Max	186	276	741	51.9	120.5	88.9	7.3	245
n	9	9	5	9	5	9	9	3
<b>immature</b>								
Mean	169	215	329	49.7	110.5	83.1	6.7	222
SD	8.43	19.57	30.18	3.19	6.88	5.05	0.62	33.68
Min	150	171	250	37.9	95.7	68.4	5.4	186
Max	184	260	372	53.9	121.8	91.7	7.9	260
n	35	34	31	35	14	31	33	6
<b>Females: adult</b>								
Mean	157	201	294	45.5	110.3	81.8	6.5	166
SD	9.47	20.48	32.37	2.77	5.76	4.63	0.64	17.30
Min	142	151	213	39.0	95.5	65.6	5.3	140
Max	185	250	359	53.2	120.3	90.5	8.3	202
n	65	61	50	65	41	62	62	14

Max	180	217	502	44.2	105.0	81.3	6.1	
n	11	11	10	11	7	11	8	
<b>immature</b>								
Mean	162	203	352	42.2	65.3	38.6	5.6	164
SD	5.93	25.57	18.36	1.17	1.64	1.43	0.36	

SD	4.77	24.60	56.94	1.38	1.73	1.90	0.28	1.23
Min	162	142	343	39.3	63.0	34.2	5.0	139
Max	180	231	519	44.2	68.6	41.3	6.1	158
n	19	19	17	19	11	19	16	5

TABLE 22. Measurements (mm) and weights (g) of specimens of *Astrapiu nigra*

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<b>Males: adult</b>								
Mean	185	399	569	41.7	69.4	41.4	6.4	
SD	3.20	16.16	45.73	0.92		0.76	0.36	
Min	179	369	518	39.0		40.1	5.9	
Max	193	437	756	43.3		42.4	7.0	
n	25	24	23	25	1	22	24	
<b>subadult</b>								
Mean	182	291	361	42.2	69.5	41.7	6.5	
SD	2.04	28.47	23.02	1.47		1.18	0.39	
Min	179	273	335	39.8		40.3	6.1	
Max	185	341	398	43.8		43.8	7.2	
n	6	5	5	6	1	6	6	
<b>immature</b>								
Mean	177	266	327	41.7	70.1	41.2	6.5	190
SD	2.64	22.79	29.44	0.63	1.91	1.63	0.39	
Min	173	239	299	40.7	69.0	38.3	6.0	
Max	180	303	377	42.5	72.3	43.1	6.9	
n	6	6	6	6	3	6	6	1
<b>Females: adult</b>								
Mean	170	258	310	40.0	67.6	41.2	6.8	
SD	8.35	11.91	14.69	2.02	1.67	0.99	0.30	
Min	157	233	290	37.2	65.9	39.2	6.1	
Max	182	274	332	43.4	69.9	42.7	7.2	
n	17	15	14	17	4	17	17	

TABLE 23. Measurements (mm) and weights (g) of specimens of *Astrapia splendidissima*

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<b>Males: adult</b>								
Mean	134	161	203	37.2	65.5	39.7	6.5	
SD	1.75	6.07	5.22	0.77	0.72	1.35	0.51	
Min	131	148	193	35.3	64.7	37.7	5.6	
Max	137	175	213	38.5	66.1	42.4	7.3	
n	16	15	11	16	3	15	16	
<b>subadult</b>								
Mean	135	159	201	37.9	64.0	38.2	6.2	
SD	2.12	24.04	8.49	0.35		0.14	0.85	
Min	133	142	195	37.6		38.1	5.6	
Max	136	176	207	38.1		38.3	6.8	
n	2	2	2	2	1	2	2	
<b>immature</b>								
Mean	135	176	206	36.5	64.3	39.6	6.5	
SD	2.76	10.20	18.61	0.94	2.90	1.01	0.25	
Min	132	162	181	35.2	62.2	38.9	6.1	
Max	139	192	233	37.6	66.3	41.8	6.9	
n	7	6	5	7	2	7	7	
<b>Females: adult</b>								
Mean	132	176	204	36.3	64.4	39.2	6.8	120
SD	2.43	12.34	12.45	1.15	1.36	1.36	0.40	
Min	128	166	189	32.7	62.2	36.5	5.9	
Max	136	204	232	38.8	66.0	41.2	7.6	
n	21	19	20	21	7	21	21	1

<i>A. s. helios</i>								
<b>Males: adult</b>								
Mean	138	178	218	37.7	66.8	40.0	6.5	139
SD	2.94	21.45	14.06	1.46	0.97	1.05	0.45	0.42
Min	133	131	198	34.4	64.4	38.2	5.6	120
Max	145	201	243	39.9	68.4	42.6	7.6	149
n	22	18	18	22	5	5	21	6
<b>subadult</b>								
Mean	140	188	216	38.6	65.2	39.8	6.2	138
SD	1.79	5.57	17.93	1.53	0.88	0.65	0.45	0.745
Min	137	182	205	37.0	65.0	37.4	5.7	126
Max	142	195	237	40.2	66.4	40.6	6.9	160
n	5	4	3	5	2	4	5	2
<b>immature</b>								
Mean	143	200	231	38.0	64.9	39.5	6.5	130
SD	2.69	14.02	13.16	1.39	0.95	1.41	0.28	0.62
Min	133	165	213	35.2	64.0	37.1	6.0	106
Max	147	222	251	40.6	66.1	41.7	7.2	158
n	23	23	18	23	10	11	15	7
<b>Females: adult</b>								
Mean	137	189	212	36.8	66.3	40.3	6.6	126
SD	3.21	8.88	9.03	0.91	1.66	1.65	0.59	12.86
Min	130	173	203	34.7	64.1	38.0	5.7	104
Max	145	208	236	39.8	68.6	42.6	7.5	151
n	31	29	24	31	14	15	17	8

<i>A. s. eliottsmithi</i>								
<b>Males: adult</b>								
Mean	139	199	235	38.4	66.7	41.2	6.3	137
SD	2.43	6.89	7.78	1.40	0.85	1.23	0.51	0.65
Min	136	189	225	35.7	64.0	38.9	6.0	124
Max	142	207	243	39.8	68.9	42.2	7.7	151
n	8	5	7	8	3	3	8	3
<b>immature</b>								
Mean	139	197	226	38.7	65.5	40.1	6.1	135
SD	3.30	10.89	10.68	0.98	0.64	0.94	0.37	0.90
Min	136	182	213	37.9	65.1	37.1	5.8	111
Max	143	206	237	40.1	65.9	41.1	6.7	156
n	4	4	4	4	2	4	4	4
<b>Females: adult</b>								
Mean	136	200	224	38.0	64.2	40.3	6.5	125
SD	2.98	12.01	14.39	0.88	0.72	1.03	0.54	
Min	132	187	209	36.7	63.0	37.1	5.8	
Max	140	224	249	39.5	66.2	41.2	7.2	
n	10	10	10	10				

all subspecies								
<b>Males: adult</b>								
Mean	137	174	217	37.7	66.6	40.1	6.5	138
SD	3.21	19.61	15.50	1.29	1.03	1.05	0.45	0.88
Min	131	131	193	34.4	64.7	38.2	5.6	120
Max	145	207	243	39.9	68.4	42.6	7.6	149
n	46	38	36	46	19	13	45	12
<b>subadult</b>								
Mean	138	178	210	38.4	64.8	39.27	6.2	138
SD	3.09	18.73	15.79	1.31	0.92	0.65	0.45	17.65
Min	133	142	195	37.0	64.0	37.4	5.7	126
Max	142	195	237	40.2	66.2	40.6	6.9	160
n	7	6	5	7	5	4	7	2
<b>immature</b>								
Mean	141	195	225	37.8	64.9	39.6	6.5	132
SD	4.10	15.81	16.39	1.40	1.09	1.47	0.29	0.92
Min	132	162	181	35.2	62.2	37.1	5.8	106
Max	147	222	251	40.6	66.1	41.8	7.2	158
n	34	33	27	34	14	13	18	7
<b>Females: adult</b>								
Mean	135	187	211	36.8	65.6	39.9	6.7	125
SD	3.56	13.34	13.47	1.14	1.46	1.67	0.44	0.97
Min	128	166	197	32.7	62.7	37.1	5.7	108
Max	145	224	249	39.5	68.4	42.6	7.5	151
n	62	58	54	62	22	18	25	10

TABLE 24. Measurements (mm) and weights (g) of specimens of *Astrapia mayeri*

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<b>Males: adult</b>								
Mean	179	111	89.3	40.9	61.1	33.1	4.7	147
SD	2.74	6.55	81.76	1.73	1.37	1.49	0.29	10.52
Min	173	97	65.7	37.6	58.8	28.5	4.1	134
Max	185	126	101.7	43.2	63.6	35.0	5.2	164
n	30	29	26	29	14	25	23	12
<b>subadult</b>								
Mean	173	155	37.7	41.4	61.7	33.8	5.0	155
SD	4.77	15.27	61.80	1.65	0.66	1.11	0.29	7.07
Min	163	118	29.6	36.7	60.8	31.3	4.5	150
Max	181	176	58.0	43.3	62.2	36.9	5.5	160
n	20	19	19	20	5	19	19	2
<b>immature</b>								
Mean	165	162	30.0	40.8	60.4	33.2	5.1	148
SD	5.70	16.66	72.15	1.39	1.26	1.09	0.26	6.22
Min	156	134	15.3	39.4	59.2	31.4	4.7	143
Max	175	175	39.0	43.1	62.5	34.8	5.5	159
n	10	8	10	10	8	10	9	5
<b>Females: adult</b>								
Mean	156	152	30.9	39.4	60.9	33.0	5.0	132
SD	3.81	14.52	24.69	1.20	1.07	0.77	0.27	19.96
Min	150	122	26.0	36.4	58.8	31.4	4.4	102
Max	163	178	37.4	41.6	62.1	34.9	5.4	157
n	27	24	24	27	11	25	25	7

TABLE 25. Measurements (mm) and weights (g) of specimens of *Astrapia stephaniae*

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<b>Males: adult</b>								
Mean	171	154	64.0	41.9	66.6	38.6	5.4	160
SD	5.02	11.85	34.15	1.40	1.60	1.74	0.29	11.28
Min	160	132	57.4	37.6	64.0	33.8	4.6	144
Max	182	182	69.3	45.4	69.8	41.4	5.8	169
n	32	27	20	30	18	26	26	4
<b>subadult</b>								
Mean	171	199	39.6	42.5	65.8	38.2	5.5	
SD	4.74	19.32	48.65	1.34	1.87	1.71	0.29	
Min	163	147	34.3	39.8	63.4	35.7	5.1	
Max	180	217	50.2	44.2	68.6	41.3	6.1	
n	11	11	10	11	7	11	8	
<b>immature</b>								
Mean	162	203	35.2	42.2	65.3	38.6	5.6	164
SD	5.93	25.57	18.36	1.17	1.64	1.43	0.36	
Min	153	146	31.6	40.2	63.5	35.9	4.9	
Max	179	247	38.0	43.9	67.3	42.3	6.2	
n	19	18	16	19	8	18	18	
<b>Females: adult</b>								
Mean	156	201	32.8	40.4	65.3	38.3	5.7	148
SD	4.38	14.90	20.94	1.49	1.35	1.22	0.32	8.98
Min	145	170	27.9	36.3	63.0	36.4	4.9	136
Max	165	230	35.8	43.1	67.5	41.9	6.2	156
n	34	30	30	34	22	34	32	4

<i>A. s. feminina</i>								
<b>Males: adult</b>								
Mean	166	154	72.7	40.95		35	5.1	150
SD	4.95	44.55		0.64		1.84	0.21	
Min	162	122		40.5		33.7	4.9	
Max	169	185		41.4		36.3	5.2	
n	2	2	1	2		2	2	1
<b>subadult</b>								
Mean	166	191	39.8	42.8		37.9	5.4	147
SD	2.12	2.12	31.82	1.63		0.78	0.00	11.31
Min	164	189	37.5	41.6		37.3	5.4	139
Max	167	192	42.0	43.9		38.4	5.4	155
n	2	2	2	2		2	2	2
<b>immature</b>								
Mean	162	180	37.0	40.6	63.4	35.8	5.4	160
SD	2.50	21.52	46.79	1.41	1.56	1.11	0.29	3.5
Min	158	148	32.3	37.5	62.3	33.3	6.0	150
Max	165	201	45.7	41.9	64.5	36.9	5.8	164
n	9	7	7	9	2	9	9	3
<b>Females: adult</b>								
Mean	152	190	31.6	40.0	64.0	36.5	5.7	135
SD	6.16	19.54	31.45	1.28	1.30	0.88	0.27	4.24
Min	144	151	27.4	38.2	62.9	34.8	5.4	132
Max	165	208	35.7	42.6	66.1	37.9	6.3	139
n	9	7	7	9	5	9	9	2

<i>A. s. duvalis</i>								
<b>Males: adult</b>								
Mean	166	129	62.8	41.6	64.3	36.6	5.3	150
SD	3.89	14.22	37.76	1.64	1.27	1.57	0.34	4.50
Min	156	107	56.5	37.6	62.5	34.1	4.7	145
Max	173	158	69.1	43.8	66.4	40.0	5.8	156
n	24	20	20	24	12	24	23	4
<b>subadult</b>								
Mean	166	178	43.6	41.5	64.2	35.3	5.2	153
SD	3.39	32.73	77.42	1.33	1.01	0.76	0.20	4.62
Min	162	142	35.7	39.3	63.0	34.2	5.0	150
Max	171	231	51.9	43	65.2	36.1	5.5	158
n	6	6	5	6	4	6	6	3
<b>immature</b>								
Mean	158	196	32.2	41.8	64.4	36.7	5.3	144
SD	3.25	16.79	27.77	1.69	1.31	1.52	0.29	11.1
Min	152	158	24.6	39.3	61.6	33.2	4.8	130
Max	163	225	35.1	45.5	66.4	39	5.9	157
n	16	16	13	16	12	16	16	7
<b>Females: adult</b>								
Mean	152	185	31.7	39.4	65.0	37.1	5.6	134
SD	3.81	11.45	21.14	1.35	2.04	1.50	0.37	7.65
Min	144	157	27.8	37.0	59.9	34.1	4.7	123
Max	159	217	36.2	41.9	67.3	40.1	6.5	148
n	30	26	26	29	17	29	29	13

all subspecies								
<b>Males: adult</b>								
Mean	169	144	63.7	41.8	65.7	37.5	5.3	155
SD	5.17	18.97	38.45	1.49	1.84	1.96	0.31	9.18
Min	156	107	56.5	37.6	62.5	33.7	4.6	144
Max	182	185	72.7	45.4	69.8	41.4	5.8	169
n	58	49	41	56	30	52	51	9
<b>subadult</b>								
Mean	168	192	40.8	42.2	65.2	37.2	5.4	150
SD	4.77	24.60	56.94	1.35	1.73	1.90	0.28	7.23
Min	162	142	34.3	39.3	63.0	34.2	5.0	139
Max	180	231	51.9	44.2	68.6	41.3	6.1	158
n	19	19	17	19	11	19	16	6
<b>immature</b>								
Mean	160	196	34.5	41.8	64.6	37.3	5.5	150
SD	4.93	22.80	33.59	1.52	1.51	1.80	0.35	12.3
Min	152	146	24.6	37.5	61.6	33.2	4.8	130
Max	179	247	45.7	46.5	67.3	42.3	6.2	164
n	44	41	36	44	22	43	43	11
<b>Females: adult</b>								
Mean	154	193	32.2	40.0	65.1	37.6	5.7	137
SD	4.68	15.89	22.62	1.47	1.66	1.45	0.34	9.47
Min	144.0	151.0	26.8	36.3	59.9	34.1	4.7	123
Max	165	230	36.2	43.1	67.5	41.9	6.5	159
n	73	63	63	72	44	71	70	19

TABLE 26. Measurements (mm) and weights (g) of specimens of *Astropia rothschildi*.

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<b>Males: adult</b>								
Mean	188	352	443	41.8	67.1	39.2	6.7	207
SD	3.35	30.02	33.19	1.38	1.62	1.04	0.40	17.46
Min	182	271	367	38.0	65.0	37.2	5.5	186
Max	194	387	486	44.1	71.8	40.8	7.2	225
n	25	20	16	25	15	24	23	5
<b>subadult</b>								
Mean	178	227	270	42.3	65.6	38.0	6.2	
SD	0.00	14.14	6.36	0.85	0.85	1.77		
Min	178	217	265	41.7	65.0	36.7		
Max	178	237	274	42.9	66.2	39.2		
n	2		2	2	2	2	1	
<b>immature</b>								
Mean	169	225	255	41.4	64.6	39.1	7.3	197
SD	6.62	16.68	27.67	1.37		0.75	0.59	2.8
Min	158	202	231	39.2		38.1	6.7	185
Max	176	241	283	42.7		37.9	8	199
n	4	4	4	5	1	4	5	2
<b>Females: adult</b>								
Mean	164	220	256	40.1	65.2	39.3	6.9	159
SD	8	8	11	1.23	1.28	1.28	0.30	17.97
Min	152	208	240	38.6	62.4	36.5	6.1	143
Max	180	233	283	43.5	66.9	41.2	7.5	200
n	21	19	16	20	11	21	21	

TABLE 27. Measurements (mm) and weights (g) of specimens of *Lophorina superba*

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<i>L. s. superba</i>								
<b>Males: adult</b>								
Mean	140	99	102	31.2	56.5	30.2	5.2	90
SD	3.57	2.60	3.17	1.06	0.83	0.97	0.46	4.60
Min	131	93	97	28.0	55.3	28.2	4.4	81
Max	149	104	109	32.6	57.9	32.5	6.2	95
n	24	23	20	23	12	23	23	8
<b>subadult</b>								
Mean	139	102	104	31.4		30.8	5.8	
SD	1.53	2.00	2.12	0.49		0.36	0.10	
Min	138	100	102	31.1		30.4	5.7	
Max	141	104	105	32.0		31.1	5.9	
n	3	3	2	3		3	3	
<b>immature</b>								
Mean	134	101	104	31.2	56.7	29.7	5.5	
SD	2.30	2.12	2.14	0.47	0.92	0.56	0.57	
Min	129	98	101	30.6	56.0	28.9	4.9	
Max	135	104	107	31.7	57.3	30.4	6.3	
n	7	7	7	7	2	7	6	
<b>Females: adult</b>								
Mean	126	96	98	30.0	55.5	30.2	5.6	74
SD	3.17	3.36	4.27	1.11	0.94	1.39	0.47	7.12
Min	122	90	93	28.3	54.4	26.2	4.9	68
Max	133	103	110	32.0	57.0	32.1	6.8	85
n	16	16	16	15	7	16	15	6

	<i>L. s. minor</i>							
Males: adult								
Mean	132	85	88	31.5	55.5	30.0	5.2	83
SD	3.43	2.95	3.33	1.02	1.56	1.30	0.31	5.08
Min	126	80	82	28.1	53.4	27.7	4.6	77
Max	140	92	94	33.3	58.5	33.5	6.2	93
n	33	33	32	32	13	31	32	8
subadult								
Mean	130	85	87	31.5	54.8	29.5	5.4	72
SD	2.29	3.01	2.75	1.26	1.12	1.02	0.32	
Min	125	80	81	28.8	52.6	28.6	5.0	
Max	134	89	92	33.6	55.8	32.1	6.1	
n	12	12	12	12	7	12	12	1
immature								
Mean	122	85	87	31.3	55.1	29.6	5.3	72
SD	4.53	4.34	4.90	1.09	0.56	0.43	0.28	7.93
Min	117	77	77	29.1	54.2	29.1	4.8	67
Max	131	91	92	32.6	55.8	30.5	5.8	84
n	14	13	13	14	8	13	12	4
Females: adult								
Mean	116	80	81	28.7	53.6	29.2	5.3	63
SD	3.85	3.81	4.03	1.37	1.34	1.18	0.24	4.65
Min	110	71	73	26.6	50.9	27.5	4.7	56
Max	126	88	91	32.1	55.5	31.3	5.7	68
n	24	23	21	24	17	24	24	

<i>L. s. latipennis</i>								
<b>Males: adult</b>								
Mean	136	91	95	32.3	55.6	29.3	5.3	85
SD	2.84	3.32	3.24	0.93	0.99	0.95	0.34	2.65
Min	132	85	90	30.4	54.9	27.8	4.9	85
Max	145	97	102	34.6	57.6	31.7	6.1	92
n	21	21	18	21	6	21	20	9
<b>subadult</b>								
Mean	134	90	91	32.0	56.5	29.5	5.4	87
SD	0.71	4.24	5.66	0.14		1.56	0.57	
Min	133	87	87	31.9		28.4	5.0	
Max	134	93	95	32.1		30.6	5.8	
n	2	2	2	2	1	2	2	1
<b>immature</b>								
Mean	129	87	88	30.4	54.2	28.3	5.2	80
SD	3.61	1.73	2.52	0.72	0.42	0.17	0.21	
Min	125	85	86	29.8	53.9	28.1	5.0	
Max	132	88	91	31.2	54.5	28.4	5.3	
n	3	3	3	3	2	3	2	1
<b>Females: adult</b>								
Mean	117	82	83	29.6	54.3	29.1	5.3	67
SD	2.36	2.30	2.57	1.05	2.04	1.07	0.23	6.20
Min	114	73	78	27.6	52.2	27.9	4.9	54
Max	124	87	87	31.0	58.4	30.7	5.7	77
n	14	13	13	14	8	14	14	

<i>L. s. femina</i>								
<b>Males: adult</b>								
Mean	139	87	88	32.4	56.2	30.7	5.4	81.0
SD	2.95	3.47	3.37	1.11	0.88	0.90	0.26	13.0
Min	134	82	83	29.7	54.5	28.7	4.8	60.0
Max	146	99	99	34.3	57.7	32.6	5.8	95.0
n	27	27	26	26	12	28	27	5
<b>subadult</b>								
Mean	139	84	85	33.1		31.0	5.8	
SD	2.16	2.45	1.53	1.28		0.26	0.14	
Min	137	81	83	32.0		30.6	5.7	
Max	142	86	86	34.9		31.2	6.0	
n	4	4	3	4		4	4	
<b>immature</b>								
Mean	131	85	84	31.9	56.1	30.4	5.7	
SD	4.60	5.56	4.52	1.25	1.06	0.76	0.36	
Min	120	77.9	76.6	30.2	54.7	29.9	5.0	
Max	134	99	92	34.0	57.6	31.1	6.1	
n	11	10	8	11	5	11	10	

## Females: adult

Mean	122	80	80.5	29.9	55.0	31	5.7	63
SD	3.26	3.29	3.99	0.91	2.03	1.12	0.44	12.02
Min	115	73	72	28.6	52.3	28.7	4.9	54
Max	127	87	88	31.6	58.4	32.9	6.6	71
n	18	18	18	18	8	18	17	2

*L. s. niedda*

Males: adult								
Mean	139	100	101	30.4	58.2	30.9	5.4	103
SD	2.22	2.89	3.30	1.59	0.49	0.31	0.40	3.54
Min	137	97	98	28.2	57.8	30.5	5.0	100
Max	142	102	105	31.7	58.5	31.2	5.8	106
n	4	4	4	4	2	4	3	2

## Females: adult

Mean	124	100	102	30.4	55.9	30.6	5.5	71
SD	0.71	3.54	4.24	0.42	0.21	0.21	0.07	0.71
Min	123	97	99	30.1	55.7	30.4	5.4	70
Max	124	102	105	30.7	56.0	30.7	5.5	71
n	2	2	2	2	2	2	2	2

*L. s. connectens*

Males: adult								
Mean	137	88	91	31.9	55.9	29.9	5.1	87
SD	3.65	2.27	2.86	0.66	0.58	0.66	0.40	4.96
Min	128	85	85	30.8	55.3	29.0	4.6	79
Max	141	92	96	33.0	56.7	30.9	6.0	99
n	12	12	12	12	6	12	12	20

## subadult

Mean	133	92	88	31.4	55.6	29.5	5.2	77
SD	0.71	9.19	2.83	0.07	0.57	0.07	0.71	
Min	132	85	86	31.3		29.1	5.1	76
Max	133	98	90	31.4		29.9	5.2	77
n	2	2	2	2	1	2	2	2

## immature

Mean	127	86	87	31.7	55.2	29.4	5.2	77
SD	3.21	1.53	1.53	1.17	0.92	0.95	0.32	8.50
Min	123	84	85	30.4	54.5	28.8	4.8	64
Max	129	87	88	32.6	55.8	30.5	5.4	83
n	3	3	3	3	2	3	3	4

## Females: adult

Mean	118	81	82	30.2	54.2	29.9	5.4	66
SD	4.25	3.64	4.04	1.68	1.38	0.98	0.36	3.92
Min	110	77	76	28.5	51.7	28.6	5.0	61
Max	126	86	88	35.3	56.9	32.0	6.2	77
n	12	12	12	11	11	12	12	16

*L. s. sphinx*

Males: immature								
Mean	137	91	96	31.7		28.2	5.0	
n	1	1	1	1		1	1	

*L. s. addenda*

Males: adult								
Mean	136	87	89	31.6	55.7	30.1	5.3	87
SD	4.20	2.79	3.41	1.21	0.75	1.19	0.33	6.13
Min	127	81	81.9	29.1	55.0	28.4	4.6	78
Max	145	93	96	33.5	56.5	32.7	5.9	95
n	26	26	26	26	3	26	26	10

## subadult

Mean	136	91	92	32.15	56.6	30.0	5.1	79
SD	7.78	4.24	4.95	0.35	1.56	1.20	0.00	6.36
Min	130	88	88	31.9	55.5	29.1	5.1	74
Max	141	94	95	32.4	57.7	30.8	5.1	83
n	2	2	2	2	2	2	2	2

## immature

Mean	128	86	87	31.9	54.9	29.6	5.3	78
SD	4.12	3.00	2.99	1.29	1.78	1.04	0.32	5.29
Min	119	80	82	28.8	52.6	27.8	4.7	70
Max	135	91	93	34.7	57.3	31.7	5.9	86
n	19	19	18	19	7	18	18	8

## Females: adult

Mean	121	81	81	30.0	54.6	29.4	5.4	67
SD	4.59	2.32	2.81	1.64	1.50	0.98	0.21	5.42
Min	114	76	75	27.8	52.4	27.7	4.8	58
Max	131	85	88	36.5	57.5	31.4	5.8	78
n	29	29	29	29	10	29	29	13

## all subspecies

Males: adult								
Mean	136	90	92	31.8	56.1	30.1	5.3	87
SD	4.52	5.76	6.12	1.15	1.16	1.11	0.35	6.76
Min	126	80	81.9	28.0	53.4	27.7	4.4	60
Max	149	104	109	34.6	58.5	33.5	6.2	106
n	148	147	138	145	53	146	144	62

## subadult

Mean	134	88	89	31.9	55.4	29.9	5.5	78
SD	4.52	6.54	5.61	1.15	1.28	1.01	0.35	5.71
Min	125	80	81	28.8	52.6	28.4	5.0	72
Max	142	104	105	34.9	57.7	32.1	6.1	87
n	26	26	24	26	11	26	26	6

## immature

Mean	128	87	89	31.6	55.3	29.7	5.4	76.2
SD	5.46	6.32	6.96	1.15	1.24	0.89	0.37	6.58
Min	117	77	76.6	28.8	52.6	27.8	4.7	64
Max	137	104	107	34.7	57.6	31.7	6.3	86
n	58	56	53	58	26	56	52	17

## Females: adult

Mean	120	83	84	29.7	54.4	29.7	5.5	67
SD	4.96	6.50	7.33	1.43	1.60	1.19	0.36	5.77
Min	110	71	72	26.6	50.9	26.2	4.7	54
Max	133	103	110	36.5	58.4	32.9	6.8	85
n	117	115	113	115	63	117	115	52

TABLE 28. Measurements (mm) and weights (g) of specimens of *Parotia waltoni*

Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
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Males: adult							
Mean	161	187	213	50.9	59.6	30.8	6.6
SD	2.66	8.93	6.91	1.41	2.08	1.13	0.46
Min	157	159	201	48.5	56.4	28.8	5.6
Max	166	198	225	53.2	62.0	32.7	7.3
n	21	19	16	21	9	18	19

## subadult

Mean	160	161	182	52.1	59.7	31.4	6.7
SD	1.00	11.93	2.00	0.70		1.85	0.06
Min	159	148	180	51.4		29.3	6.7
Max	161	171	184	52.8		32.8	6.8
n	3	3	3	3	1	3	3

## immature

Mean	157	161	175	48.9	61.5	31.9	6.7
SD	2.87	10.34	6.29	3.06	1.73	1.10	0.58
Min	152	140	165	42.8	59.3	30.7	6.2
Max	161	172	184	51.7	63.5	32.9	7.5
n	8	7	7	8	4	4	4

## Females: adult

Mean	149	153	166	46.3	60.7	31.1	7.1
SD	3.83	5.80	3.60	2.41	1.09	1.23	0.52
Min	142	140	161	43.5	59.1	27.6	6.1
Max	157	164	175	52.1	62.4	33.3	7.8
n	20	19	17	20	11	19	19



TABLE 29. Measurements (mm) and weights (g) of specimens of  
*Parotia setilata*

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<b>Males: adult</b>								
Mean	166	128	130	52.8	67.1	35.3	5.7	192
SD	2.41	2.84	3.27	1.63	1.34	1.93	0.37	10.30
Min	161	123	125	49.9	64.0	30.4	5.0	175
Max	170	133	137	56.6	68.9	39.5	6.4	205
n	32	30	29	31	14	31	24	12
<b>subadult</b>								
Mean	165	131	133	52.2	67.2	36.1	6.1	202
SD	1.75	3.49	4.41	2.78	1.45	0.88	0.44	7.6
Min	162	126	125	43.9	65.6	34.2	5.4	195
Max	168	139	142	55.1	69.6	37.5	6.9	210
n	15	15	14	15	7	13	13	3
<b>immature</b>								
Mean	162	133	136	52.9	67.1	36.5	6.0	183
SD	3.59	4.03	4.78	1.61	1.15	1.16	0.43	14.8
Min	154	121	122	44.4	62.9	30.3	5.4	140
Max	167	138	147	56.4	68.5	38.0	6.8	200
n	17	17	17	17	4	16	15	5
<b>Females: adult</b>								
Mean	152	128	129	47.5	65.2	35.0	6.1	172
SD	4.16	3.17	3.03	2.35	1.24	1.66	0.49	12.86
Min	141	121	122	44.4	62.9	30.3	5.4	140
Max	163	135	134	54.1	67.5	37.0	7.5	185
n	26	25	24	24	18	25	25	14

TABLE 30. Measurements (mm) and weights (g) of specimens of  
*Parotia carolae*

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<b>Males: adult</b>								
Mean	154	75	76	50.1	61.5	34.9	7.2	
SD	1.34	2.52	1.56	1.25	0.72	2.23	0.36	
Min	152	73	73	48.3	60.9	30.5	6.7	
Max	156	82	78	52.6	62.2	37.6	8.1	
n	12	12	12	12	4	10	12	
<b>subadult</b>								
Mean	153	85	81	50.0	62.6	37.3	7.0	
SD	2.57	5.26	6.16	1.54	1.01	1.75	0.46	
Min	148	74	75	48.1	61.5	34.5	6.2	
Max	157	90	95	52.6	63.5	40.1	7.9	
n	12	12	9	11	3	12	12	
<b>Females: adult</b>								
Mean	143	91	91	45.4	61.6	36.7	7.3	
SD	3.41	2.93	2.81	1.07	1.63	1.72	0.29	
Min	133	87	87	43.4	59.1	33.7	6.9	
Max	146	96	95	47.1	63.4	39.1	7.9	
n	13	13	11	13	7	12	12	
<b>P. c. beilepschi</b>								
<b>Males: adult</b>								
Mean	156	77	75	47.3	57.9	34.2	6.8	
SD		0.00	0.00	0.14		2.26	0.64	
Min	156	77	75	47.2		32.6	6.3	
Max	156	77	75	47.4		35.8	7.2	
n	2	2	2	2	1	2	2	

<b>subadult</b>							
Mean	152	92	85	49.25	61.1	33.0	6.8
SD		2.83	5.66	0.35		0.64	0.14
Min		90	81	49		32.5	6.7
Max		94	89	49.5		33.4	6.9
n	1	2	2	2	1	2	2

*P. c. meeki*

<b>Males: adult</b>							
Mean	153	76	75	50.8		37.9	6.7
SD	1.50	2.16	1.26	0.66		1.48	0.30
Min	151	73	73	50.0		36.8	6.4
Max	154	78	76	51.5		38.9	7.1
n	4	4	4	4		2	4
<b>subadult</b>							
Mean	150	84	81	50.3	63.2	38.0	6.9
SD	4.06	4.76	4.80	1.27	0.39	3.42	0.41
Min	142	75	75	48.6	62.8	34.1	6.3
Max	157	89	89	52.1	63.6	42.2	7.4
n	9	9	8	9	4	5	8
<b>immature</b>							
Mean	148	91		48.1			7
SD	0.71	4.95		2.12			
Min	147	87		46.6			
Max	148	94		49.6			
n	2	2		2			1
<b>Females: adult</b>							
Mean	141	91	90	46.3	62.2	37.6	7.4
SD	2.83	2.61	2.77	1.14	1.15	1.43	0.45
Min	136	86	85	44.6	60.5	34.6	6.5
Max	146	96	95	47.9	63.9	38.6	8.1
n	12	12	11	11	6	7	12

*P. c. chalciothorax*

<b>Males: adult</b>							
Mean	159	77	76	51.7	61.1	33.6	7.3
SD	1.41	2.83	2.83	0.99			
Min	158	75	74	51			
Max	160	79	78	52.4			
n	2	2	2	2	1	1	1
<b>subadult</b>							
Mean	157	92	85	51.3	61.0	34.3	7.7
SD	1.00	9.54	5.00	0.81	1.22	2.12	0.21
Min	156	81	80	50.6	59.7	32.8	7.5
Max	158	98	90	52.2	62.1	35.8	7.9
n	3	3	3	3	3	2	3
<b>Females: adult</b>							
Mean	146	93	92	45.2	58.9	35.1	7.5
SD	1.14	1.95	1.83	1.42	0.85	1.60	0.94
Min	145	90	90	43.0	57.9	32.7	6.5
Max	148	95	94	46.5	59.5	36.2	8.8
n	5	5	4	5	3	4	5

*P. c. chrysenia*

<b>Males: adult</b>							
Mean	159	82	82	52.6	61.5	36.8	7.4
SD	0.71	0.71	0.71	0.57			0.57
Min	158	81	81	52.2			7
Max	159	82	82	53.0			7.6
n	2	2	2	2	1	1	2
<b>subadult</b>							
Mean	155	94	92	49.9	60.1	34.5	7.4
SD	2.08	5.69	1.53	1.01	1.10	1.62	0.45
Min	153	88	91	49.0	58.8	32.6	7.0
Max	157	99	94	51.0	60.8	35.5	7.9
n	3	3	3	3	3	3	3
<b>immature</b>							
Mean	153	99	99	49.5	63.2	33.9	7.6
SD	2.12	1.41	0.71	2.05		1.34	0.14
Min	151	98	98	48		32.9	7.5
Max	154	100	99	50.9		34.8	7.7
n	2	2	2	2	1	2	1

Females: adult								
Mean	147	95	95	47.0	61.6	34.2	8.2	130
SD	4.65	1.73	2.65	0.90	0.98	2.58	0.35	21.13
Min	138	91	90	45.1	60.1	29.4	7.6	110
Max	154	97	99	48.2	62.8	37.0	8.6	152
n	9	9	9	9	7	6	9	3

<i>P. c. clelandiae</i>								
Males: adult								
Mean	157	80	80	50.3	62.5	31.9	7.4	205
SD	4.50	3.14	2.66	1.68	0.83	0.72	0.53	
Min	149	77	77	48.6	61.6	30.6	6.7	
Max	161	86	83	52.9	63.6	32.7	8.1	
n	8	8	6	7	4	6	8	1
subadult								
Mean	154	89	87	52		36.4	6.9	211
SD	5.57	7.51	9.19	1.20		0.71	0.42	
Min	148	84	80	51.2		35.9	6.4	
Max	159	98	93	52.9		36.9	7.2	
n	3	3	2	2		2	3	1
immature								
Mean	152	98	98	51.8	63.6	37.0	7.2	
SD	0.58	4.04	4.04	1.98		0.17	0.10	
Min	151	94	94	49.7		36.8	7.1	
Max	152	102	102	53.6		37.1	7.3	
n	3	3	3	3	1	3	3	
Females: adult								
Mean	147	94	94	48.6	62.3	36.2	7.9	163
SD	4.64	2.30	1.79	2.67	1.03	1.37	0.46	
Min	141	91	93	45.9	61.2	35.2	7.1	
Max	153	97	97	51.7	63.2	39.5	8.3	
n	5	5	5	5	3	5	5	1

all subspecies								
Males: adult								
Mean	155	77	77	50.3	61.5	34.3	7.2	205
SD	3.21	3.31	2.80	1.59	1.43	2.45	0.46	
Min	149	73	73	47.2	57.9	30.5	6.3	
Max	161	86	83	53.0	63.6	38.9	8.1	
n	30	30	28	29	11	22	29	1
subadult								
Mean	153	87	83	50.3	61.8	36.5	7.0	211
SD	3.67	6.46	6.25	1.37	1.48	2.51	0.46	
Min	142	74	75	48.1	58.8	32.5	6.2	
Max	159	99	95	52.9	63.6	42.2	7.9	
n	31	32	27	30	14	26	31	1
immature								
Mean	151	96	98	50.1	63.4	35.7	7.3	210
SD	2.43	4.93	2.92	2.39	0.28	1.86	0.26	
Min	147	87	94	46.6	63.2	32.9	7.0	
Max	154	102	102	53.6	63.6	37.1	7.7	
n	7	7	5	7	2	5	6	1
Females: adult								
Mean	144	92	92	46.3	61.5	36.2	7.6	138
SD	4.29	2.89	3.17	1.68	1.52	2.05	0.56	24.0
Min	133	86	85	43	57.9	29.4	6.5	110
Max	154	97	99	51.7	63.9	39.1	8.8	163
n	41	44	40	43	26	34	43	4

TABLE 31. Measurements (mm) and weights (g) of specimens of *Parotia lawesii*

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<i>P. l. lawesii</i>								
Males: adult								
Mean	154	80	79	49.7	63.6	33.3	5.3	
SD	2.33	2.33	1.75	1.86	1.26	1.12	0.67	
Min	143	73	76	45.7	61.9	30.3	4.4	
Max	161	84	83	52.3	67.1	36.6	6.4	
n	23	25	16	23	20	24	9	
subadult								
Mean	154	89	88	50.2	63.0	33.2	5.3	
SD	2.84	6.61	6.22	1.56	0.49	1.18	0.62	
Min	144	80	76	47.3	62.0	30.1	4.7	
Max	161	100	97	52.3	63.7	36.6	6.4	
n	13	17	16	16	12	11	11	
immature								
Mean	152	98	98	49.4	62.9	33.0	5.5	
SD	3.65	3.32	3.88	2.38	1.80	1.07	0.51	
Min	144	91	92	44.5	60.5	31.4	4.6	
Max	157	103	104	52.8	66.0	36.6	6.4	
n	13	13	11	12	7	12	11	
Females: adult								
Mean	150	99	97	47.8	62.5	33.6	5.7	141
SD	5.52	3.04	3.36	3.30	0.97	1.64	0.36	
Min	144	94	92	43.9	61.3	30.9	5.1	
Max	159	102	101	52.8	64.3	36.9	6.4	
n	11	11	10	11	10	11	10	
<i>P. l. helenae</i>								
Males: adult								
Mean	154	80	80	49.4	64.5	34.0	5.6	170
SD	2.49	2.29	1.06	1.69	1.48	2.32	0.49	5.94
Min	143	76	78	45.7	61.9	28.9	5.1	160
Max	161	84	82	53.1	68.8	36.6	6.5	174
n	23	23	12	22	17	22	11	5
subadult								
Mean	154	91	79	49.7	65.5	34.7	5.4	180
SD	2.49	11.39	7.07	1.14	0.99	1.63	0.37	2.78
Min	142	75	74	48.5	63.1	31.8	4.6	164
Max	161	103	84	51.5	66.5	36.6	6.4	195
n	7	6	2	6	6	6	6	2
immature								
Mean	150	98	100	49.5	63.9	33.5	5.4	167
SD	2.77	3.71	2.52	1.40	1.42	2.64	0.45	2.16
Min	147	92	97	46.9	61.4	29.5	4.8	160
Max	154	102.6	102	51.0	65.4	36.4	6.1	173
n	9	9	3	8	8	9	9	
Females: adult								
Mean	148	99	98	46.7	65.1	35.3	6.1	149
SD	3.71	3.17	3.42	1.78	0.54	0.82	0.11	9.49
Min	143	95	95	44.9	64.2	33.9	5.2	138
Max	156	107	105	51.1	65.9	36.1	7.2	159
n	14	14	8	14	13	13	13	5
<i>P. l. fuscior</i>								
Males: adult								
Mean	157	80	80	49.1	62.8	33.1	4.7	167
SD		2.09	0.00	1.23	0.82	1.21	0.41	1.81
Min	143	76	80	47.6	62.1	28.4	4.1	150
Max	161	82	80	51.0	63.9	35.9	5.1	171
n	7	7	2	7	6	7	7	4
subadult								
Mean	157	84		49.7	63.9	32.9	4.8	
n	1	1		1	1	1	1	
immature								
Mean	153	96	95	51.2	62.1	33.1	5.6	164
n	1	1	1	1	1	1	1	14

## Females: adult

Mean	147	98	94	44.0	61.8	31.2	5.1	143
SD	4.77	2.80		2.24	1.01	1.99	0.41	8.39
Min	141	92		40.3	60.6	26.0	4.6	122
Max	157	102.4		48.9	62.8	33.7	6.2	169
n	13	13	1	13	4	13	13	55

*P. l. exhibit*

## Males: adult

Mean	157	79	80	49.8	62.4	33.1	5.2	175
SD	2.71	2.77	1.71	1.60	1.25	1.95	0.68	
Min	152	75	77	47.0	60.1	29.9	4.0	
Max	161	83	82	52.8	64.1	35.3	6.5	
n	12	12	8	12	8	12	11	1

## subadult

Mean	157	92	90	51.1		32.1	5.6	179
SD	2.83	1.41	1.41	0.64		0.42		
Min	155	91	89	50.6		31.8		
Max	159	93	91	51.5		32.4		
n	2	2	2	2		2	1	1

## immature

Mean	153	100	100	51.5	62.4	32.6	5.3	173
SD	2.30	3.34	2.77	1.22	2.02	2.89	0.43	6.38
Min	150	94	97	50.2	59.5	27.0	4.8	168
Max	157	104	104	53.5	65.3	35.1	5.9	180
n	7	7	5	7	6	7	7	4

## Females: adult

Mean	145	97	96	45.6	62.2	31.8	5.6	154
SD	1.57	2.90	2.39	0.88	1.04	2.28	0.42	11.15
Min	143	93	92	44.4	61.2	27.1	5.0	139
Max	147	103	98	46.9	63.6	34.4	6.5	166
n	10	10	5	10	4	10	10	4

## all subspecies

## Males: adult

Mean	155	80	80	49.6	63.6	33.5	5.3	167
SD	3.23	2.36	1.48	1.67	1.47	2.05	0.61	7.55
Min	148	73	76	45.7	60.1	28.9	4.0	153
Max	163	84	83	53.1	68.8	38.6	6.9	195
n	68	67	38	64	51	65	57	53

## subadult

Mean	155	90	87	50.1	63.9	33.4	5.3	179
SD	2.86	7.50	6.43	1.40	1.33	1.51	0.47	5.51
Min	149	75	74	47.3	62.0	31.0	4.7	174
Max	160	103	97	52.3	66.5	36.6	6.9	185
n	26	26	20	25	19	26	24	3

## immature

Mean	152	99	99	50.0	63.1	33.0	5.4	166
SD	3.27	3.37	3.49	2.01	1.74	1.88	0.45	8.45
Min	144	91	92	44.5	59.5	27.0	4.6	151
Max	157	104	104	53.5	66.0	36.4	6.6	180
n	30	30	20	28	22	29	28	20

## Females: adult

Mean	148	98	97	46.0	63.4	33.0	5.6	144
SD	4.40	2.97	3.14	2.58	1.61	2.36	0.59	8.92
Min	141	92	92	40.3	60.6	26.0	4.6	122
Max	159	107	105	52.8	65.9	36.3	7.3	169
n	48	48	24	48	31	47	47	65

TABLE 32. Measurements (mm) and weights (g) of specimens of *Pteridophora alberti*

	Wing length	Tail length	Tarsus length	Total head length	Bill length	Bill width	Weight
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## Males: adult

Mean	124	85	32.2	49.4	24.6	5.2	84
SD	2.46	3.43	1.37	1.02	0.97	0.37	3.78
Min	120	79	29.5	47.9	22.7	4.6	80
Max	129	97	35.1	51.3	26.5	6.1	89
n	26	26	25	11	25	25	5

## subadult

Mean	124	87	32.5	48.1	23.4	4.8	
n	1	1	1	1	1	1	

## immature

Mean	120	86	32.5	49.4	24.4	5.3	78
SD	3.74	3.53	1.06	0.91	1.16	0.32	5.06
Min	112	78	30.6	48.6	21.4	4.8	72
Max	125	91	34.4	50.9	25.7	5.9	84
n	12	12	10	5	12	11	4

## Females: adult

Mean	113	82	30.6	48.1	24.0	5.5	75
SD	1.95	2.59	1.09	1.12	0.97	0.33	4.93
Min	108	77	28.8	45.6	22.4	4.8	68
Max	117	87	32.8	49.6	26.2	6.1	83
n	25	25	25	13	25	24	8

*P. a. burgersi*

## Males: adult

Mean	125	85	32.6	48.5	24.3	5.3	
SD	5.57	2.52	1.68		2.23	0.32	
Min	119	82	31.5		21.9	4.9	
Max	130	87	34.5		26.3	5.5	
n	3	3	3	1	3	3	

## immature

Mean	119	86	31.2	47.2	23.1	5.3	93
SD	5.56	3.42	1.87	1.06	0.32	0.54	
Min	113	81	29.5	46.2	22.8	4.9	
Max	124	89	33.4	48.3	23.4	6.1	
n	4	4	4	3	4	4	1

## Females: adult

Mean	114	83	29.8	47.9	24.8	5.4	73
SD	2.00	2.74	0.56	3.61	0.96	0.23	
Min	111	79	29.3	45.3	23.4	5.2	
Max	116	86	30.4	50.4	25.7	5.8	
n	5	5	5	2	5	5	1

*P. a. halstromi*

## Males: adult

Mean	127	88	32.1	50.5	24.3	5.0	90
SD	3.38	2.36	0.75	1.62	1.11	0.31	4.34
Min	122	82	30.6	47.1	21.6	4.4	83
Max	133	94	33.5	52.5	26.4	5.7	95
n	24	25	25	14	24	23	8

## subadult

Mean	122	89	32.1	50.2	24.4	4.9	92
SD	5.77	3.54	1.04	0.28	0.88	0.43	
Min	114	83	30.6	50.0	23.6	4.3	
Max	128	92	33.3	50.4	25.8	5.5	
n	5	5	5	2	5	5	1

## immature

Mean	123	90	32.1	48.4	24.1	5.1	80
SD	3.85	2.15	1.1	1.08	1.27	0.44	7.7
Min	116	81	30.4	47.2	22.5	4.4	71
Max	127	91	34.4	50.4	26.5	6.1	90
n	14	14	11	12	15	21	7

<b>Females: adult</b>								
Mean	118	86	31.0	48.5	24.0	5.7	84	
SD	4.68	3.41	1.33	1.67	0.94	0.42	15.1	
Min	109	80	28.1	45.8	23.1	4.7	74	
Max	128	91	34.0	51.3	25.8	6.4	94	
n	15	15	15	7	14	14	15	
<b>all subspecies</b>								
<b>Males: adult</b>								
Mean	126	86	32.2	50.0	24.4	5.1	87	
SD	3.36	3.26	1.13	1.47	1.10	0.35	15.0	
Min	119	79	29.5	47.1	21.6	4.4	74	
Max	133	97	35.1	52.5	26.5	6.1	94	
n	53	54	54	26	52	51	15	
<b>subadult</b>								
Mean	123	89	32.2	49.5	24.3	4.9	92	
SD	5.20	3.26	0.95	1.23	0.89	0.39		
Min	114	83	30.6	48.1	23.4	4.3		
Max	128	92	33.3	50.4	25.8	5.5		
n	6	6	6	3	6	6		
<b>immature</b>								
Mean	122	88	32.1	48.4	24.1	5.2	81	
SD	4.23	3.59	1.40	1.68	1.03	0.42	15.4	
Min	112	78	28.4	45.2	21.4	4.6	71	
Max	129	95	34.4	51.1	25.6	6.1	93	
n	40	40	37	20	39	36	12	
<b>Females</b>								
Mean	115	84	30.6	48.2	24.1	5.5	77	
SD	3.93	3.31	1.17	1.48	0.97	0.36	16.1	
Min	108	77	28.1	45.3	22.4	4.7	65	
Max	128	91	34	51.3	26.2	6.4	93	
n	45	45	45	22	44	43	12	

TABLE 33. Measurements (mm) and weights (g) of specimens of *Cicinnurus regius*

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<b><i>C. r. regius</i></b>								
<b>Males: adult</b>								
Mean	105	35	161	27.3	50.3	28.1	5.2	
SD	2.42	1.43	7.57	0.61	1.25	1.35	0.43	
Min	97	31	151	25.5	46.4	25.9	4.3	
Max	110	38	178	28.8	54	31.2	6.1	
n	26	26	26	25	24	26	26	
<b>subadult</b>								
Mean	107	51	99	27.1	51.1	28.4	5.6	
SD	1.91	12.84	34.40	0.69	0.72	1.22	0.30	
Min	105	35	59	26.3	50.2	27.0	5.1	
Max	110	68	138	27.9	52.0	30.8	6.1	
n	7	7	7	7	7	7	7	
<b>immature</b>								
Mean	104	60	61	26.2	50.5	27.5	5.6	
SD	3.35	2.19	2.46	1.20	0.69	0.50	0.34	
Min	98	56	57	22.9	49.2	26.6	4.8	
Max	110	64	64	27.5	51.1	28.3	6.1	
n	11	11	11	11.0	10.0	10.0	11	
<b>Females: adult</b>								
Mean	102	59	60	26.9	49.6	27.7	5.6	
SD	1.91	1.83	2.07	0.68	1.12	0.87	0.34	
Min	98	56	57	25.9	48.1	26.9	5.0	
Max	105	62	63	28.1	51.4	30.2	6.1	
n	15	15	14	15	14	15	15	

<b><i>C. r. rex</i></b>								
<b>Males: adult</b>								
Mean	100	31	163	26.1	48.9	26.6	4.9	53
SD	2.80	1.49	10.68	1.02	1.19	0.87	0.38	5.30
Min	96	28	142	22.2	46.5	25.2	4.2	43
Max	106	35	182	27.5	50.8	28.7	5.8	65
n	30	29	26	30	22	29	23	32
<b>subadult</b>								
Mean	103	47	78	26.3	49.2	26.4	5.1	53
SD	3.55	10.52	37.70	1.10	1.14	0.77	0.45	4.09
Min	97	30	51	24.0	47.9	25.3	4.4	48
Max	109	58.5	155	27.7	51.2	28.3	5.8	60
n	15	15	10	15	9	14	14	7
<b>immature</b>								
Mean	102	54	58	26.9	48.4	26.5	5.2	50
SD	3.09	1.94	2.81	0.65	0.72	0.73	0.49	5.20
Min	96	50	52	25.5	47.4	24.9	4.4	42
Max	107	59	62	28.0	49.6	27.9	5.9	53
n	20	20	15	20	17	19	20	4
<b>Females: adult</b>								
Mean	100	56	57	26.0	49.5	27.0	5.4	49
SD	3.07	2.59	2.97	0.77	0.94	1.27	0.48	6.75
Min	94	50	51	24.7	47.2	24.7	4.1	38
Max	107	61	61	27.5	50.9	30.4	6.4	58
n	28	28	23	28	23	28	28	10

<b><i>C. r. coccineifrons</i></b>								
<b>Males: adult</b>								
Mean	102	34	158	26.5	48.2	25.9	5.1	54
SD	1.37	1.75	10.56	0.67	1.57	0.60	0.28	3.31
Min	100	32	136	24.9	46.5	25.1	4.7	51
Max	105	37	170	27.5	50.2	27.3	5.9	59
n	14	14	12	14	4	13	14	7
<b>immature</b>								
Mean	104	58	61	26.1	47.2	24.9	5.0	55
SD	1.63	1.73	1.41	0.69		1.56	0.25	
Min	102	56	59	25.5		23.3	4.7	
Max	106	60	62	27.1		26.4	5.3	
n	4	4	4	4	1	3	4	1
<b>Females: adult</b>								
Mean	102	59	60	26.9		25.6	5.1	
SD	0.71	0.71	0.00			0.42	0.07	
Min	101	58	60			25.3	5	
Max	102	59	60			25.9	5.1	
n	2	2	2	1		2	2	

<b><i>C. r. similis</i></b>								
<b>Males: adult</b>								
Mean	98	31	150	26.0	47.6	24.8	4.9	53
SD	2.19	1.44	6.07	1.03	1.50	1.20	0.32	3.61
Min	93	28	136	24.0	44.9	22.6	4.1	46
Max	102	34	160	28.0	50.4	27.6	5.6	64
n	36	35	32	35	19	35	35	40
<b>subadult</b>								
Mean	99	49	94	26.6	48.1	25.2	5.1	61
SD	1.53	7.40	40.17	0.75	0.86	0.97	0.19	3.54
Min	96	32	54	24.9	46.7	23.5	4.7	58
Max	102	55	154	27.7	49.8	27.2	5.4	63
n	16	14	8	16	11	15	14	2
<b>immature</b>								
Mean	100	54	59	26.2	47.2	24.8	5.0	54
SD	2.52	2.19	2.23	0.73	0.65	0.68	0.29	2.9
Min	96	50	56	24.5	46.2	23.5	4.4	50
Max	106	58	63	27.4	47.9	26.3	5.4	60
n	21	21	19	21	10	20	20	13
<b>Females: adult</b>								
Mean	97	55	58	26.0	48.4	25.3	5.4	52
SD	2.08	2.05	2.09	0.66	1.75	1.29	0.58	3.74
Min	93	49.1	52.9	25.0	44.4	22.6	4.4	49
Max	103	57.4	63	27.8	51.1	27.7	6.9	67
n	23	23	21	23	19	23	22	5

<i>C. r. cryptorhynchus</i>							
<b>Males: adult</b>							
Mean	101	32	155	26.5	47.5	25.3	5.2
SD	1.65	1.87	9.57	0.69	1.54	0.93	0.38
Min	99	30	139	25.2	45.4	24.0	4.7
Max	104	35	167	27.3	49.7	26.6	5.8
n	10	10	7	10	4	8	9
<b>subadult</b>							
Mean	102	44	106	26.4	48.0	24.7	5.3
SD	0.71	13.44	63.64	0.64		0.14	0.14
Min	101	34	61	25.9		24.6	5.2
Max	102	53	151	26.8		24.8	5.4
n	2	2	2	2	1	2	2
<b>immature</b>							
Mean	99	56	59	26.5	49.5	26.4	4.6
n	1	1	1	1	1	1	1
<b>Females: adult</b>							
Mean	99	56	57	25.8	48.6	25.9	5.6
SD	1.75	1.34	3.78	0.36	2.35	1.10	0.23
Min	97	54	52	25.3	46.6	25.0	5.3
Max	102	57	61	26.2	51.2	27.3	5.9
n	6	5	5	6	3	6	6
<i>C. r. gymnorhynchus</i>							
<b>Males: adult</b>							
Mean	99	30	161	26.5	48.1	26.6	5.2
SD	2.22	1.74	13.07	0.74	1.37	0.71	0.44
Min	93	28	134	24.8	46.0	25.3	4.5
Max	105	35	177	28.1	49.8	27.7	5.9
n	25	24	18	24	8	24	21
<b>subadult</b>							
Mean	100	46	143	26.1	48.8	26.9	5.3
SD	0.71	2.83	26.87	0.00	1.77	1.27	0.49
Min	99	44	124	26.1	47.5	26	4.9
Max	100	48	162	26.1	50.0	27.8	5.6
n	2	2	2	2	2	2	2
<b>Females: adult</b>							
Mean	98	53	57	25.8	49.9	27.8	5.7
SD	1.58	3.02	1.58	0.63	1.72	2.03	0.42
Min	96	50	55	25.4	48.0	25.0	5.1
Max	100	57.3	59	26.9	51.4	30.3	6.2
n	5	5	5	5	3	5	5
all subspecies							
<b>Males: adult</b>							
Mean	100	32	158	26.4	48.8	26.3	5.1
SD	3.34	2.21	10.49	0.96	1.68	1.53	0.41
Min	93	28	134	22.2	44.9	22.6	4.1
Max	110	38	182	28.8	54.0	31.2	6.1
n	141	138	121	138	81	135	128
<b>subadult</b>							
Mean	102	48	94	26.6	49.2	26.2	5.2
SD	3.69	9.54	39.59	0.88	1.49	1.48	0.37
Min	96	30	51	24.0	44.7	23.5	4.4
Max	110	68	162	27.9	52	30.8	6.1
n	42	40	29	42	30	40	39
<b>immature</b>							
Mean	102	55	59	26.5	48.6	26.0	5.2
SD	3.29	3.16	2.70	0.86	1.39	1.27	0.44
Min	96	50	52	22.9	46.2	23.3	4.4
Max	110	64	64	28.0	51.1	28.3	6.1
n	57	57	50	57	39	53	56
<b>Females: adult</b>							
Mean	99	56	58	26.2	49.2	26.6	5.5
SD	2.96	2.86	2.44	0.77	1.43	1.57	0.47
Min	93	49.1	51	24.7	44.4	22.6	4.1
Max	107	62	63	28.1	51.4	30.4	6.9
n	79	78	70	78	62	79	78

TABLE 34. Measurements (mm) and weights (g) of specimens of *Cicinnurus magnificus*

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<i>C. m. magnificus</i>								
<b>Males: adult</b>								
Mean	116	39	269	31.9	54.675	28.9	7.0	97
SD	2.61	2.05	23.03	1.09	1.03	1.12	0.44	6.82
Min	111	35	213	28.9	53.2	26.2	6.2	85
Max	121	43	319	33.9	56.5	31.3	7.9	110
n	26	25	21	25	12	25	25	13
<b>subadult</b>								
Mean	115	55	157	30.8	56.1	29.2	7.4	
SD	2.28	7.23	109.47	0.59		0.90	0.34	
Min	112	42	61	29.9		27.9	6.8	
Max	117	59	256	31.5		29.9	7.6	
n	5	5	4	5	1	4	5	
<b>immature</b>								
Mean	117	60	64	31.4	55.2	29.3	7.0	88
SD	3.74	1.22	2.66	1.42	1.48	0.55	0.48	8.84
Min	114	58	60	29.6	54.1	28.5	6.4	82
Max	124	61	67	33.5	56.2	29.9	7.6	94
n	6	6	6	6	2	6	6	2
<b>Females: adult</b>								
Mean	113	61	63	30.4	54.2	29.3	7.0	79
SD	2.76	2.79	4.11	1.49	0.95	1.28	0.39	6.26
Min	108	56	57	27.6	53.2	27.5	6.0	73
Max	117	66	69	33.4	55.8	32.7	7.7	89
n	16	16	14	16	8	16	16	7
<i>C. m. chrysopleus</i>								
<b>Males: adult</b>								
Mean	116	39	294	31.4	55.7	29.7	7.0	102
SD	1.88	2.17	19.64	1.06	1.24	1.05	0.25	6.30
Min	112	33	256	28.6	53.6	27	6.6	92.0
Max	120	42	321	33.0	57.1	31.9	7.6	119.0
n	24	22	19	23	7	22	23	36
<b>immature</b>								
Mean	116	61	64	31	56	30	7	98
SD	2.47	3.27	3.54	0.65	0.69	0.83	0.38	6.67
Min	111	56	57	30.0	54.6	28.5	6.2	74.0
Max	120	69	72	32.2	56.4	32.2	7.9	108.0
n	19	19	19	19	7	19	19	24
<b>Females: adult</b>								
Mean	112	60	62	30.2	55.4	29.4	7.1	91
SD	4.24	1.95	4.28	1.13	1.12	1.06	0.33	7.93
Min	107	57	65	27.9	53.9	26.4	6.4	81.0
Max	125	63	69	32.9	57.3	31.3	7.6	113.0
n	20	20	16	20	8	20	20	23
<i>C. m. hunsteini</i>								
<b>Males: adult</b>								
Mean	113	39	272	31.2	56.3	30.7	6.6	90.9
SD	2.42	1.83	19.88	1.04	0.88	0.70	0.35	8.21
Min	105	35	225	28.8	54.8	28.9	5.9	74.5
Max	117	43	303	33.1	58.4	32.7	7.3	105
n	38	38	32	35	24	37	38	33
<b>subadult</b>								
Mean	112	54	61	31.7	56.6	30.2	6.9	91
SD	5.15	4.09	1.94	1.99	1.36	1.70	0.55	
Min	104	47	58	28.3	55.1	26.9	6.0	
Max	120	58	64	35.1	58.2	31.8	7.8	
n	8	8	6	8	5	8	8	1
<b>immature</b>								
Mean	112	59	63	31.9	55.8	30.2	6.6	87
SD	2.99	2.73	2.98	0.87	0.86	0.66	0.14	8.40
Min	105	54	59	30.1	53.8	28.8	0.5	72
Max	117	67.4	71	35.2	57.7	31.7	7.7	103
n	12	13	12	13	6	14	14	21

## Females: adult

Mean	108	59	60	30.0	55.4	30.4	6.9	77
SD	2.09	2.35	3.15	1.05	0.89	0.77	0.33	8.79
Min	104	53.9	53.3	26.5	53.9	28.6	6.3	62
Max	115	64	66	32.0	57.1	31.8	7.8	94
n	45	44	31	45	22	45	44	37

*C. m. intermedius*

## Males: adult

Mean	115	38	258	32.0	56.1	30.8	7.1	
SD	1.71	2.58	17.02	0.85	1.41	1.60	0.30	
Min	112	35	229	30.2	54.5	28.7	6.5	
Max	118	44	287	33.1	57.7	34.5	7.7	
n	16	16	10	16	4	15	14	

## subadult

Mean	119	55		31.5		30.4	7.2	
SD	3.54	0.71		0.78		0.92	0.28	
Min	116	54		30.9		29.7	7.0	
Max	121	55		32.0		31.0	7.4	
n	2	2		2		2	2	

## immature

Mean	116	59	62	31.8	56.1	31.3	7.2	
SD	2.40	2.05	2.06	0.89	1.30	0.68	0.38	
Min	111	55	58.1	29.5	54.3	29.6	6.3	
Max	120	63	66	33.1	58.1	32.1	7.8	
n	18	18	17	18	8	18	17	

## Females: adult

Mean	109	59	59	29.7	55.1	30.7	7.2	
SD	2.42	2.60	2.88	0.87	0.61	0.87	0.32	
Min	104	54	53	27.6	54.0	29.1	6.6	
Max	116	63	64	31.0	56.1	32.7	7.9	
n	27	27	24	27	12	26	26	

## all subspecies

## Males: adult

Mean	115	39	275	31.5	55.8	30.0	6.9	97
SD	2.63	2.10	23.17	1.07	1.21	1.31	0.41	8.68
Min	105	33	213	28.6	53.2	26.2	5.9	74.5
Max	121	44	321	33.9	58.4	34.5	7.9	119
n	104	101	82	99	47	99	100	82

## subadult

Mean	114	54	99.2	31.4	56.5	29.9	7.1	85
SD	4.50	4.86	80.31	1.51	1.23	1.42	0.50	8.49
Min	104	42	58	28.3	55.1	26.9	6.0	79
Max	121	59	256	35.1	58.2	31.8	7.8	91
n	15	15	10	15	6	14	15	2

## immature

Mean	114	60	63	31.7	55.8	30.2	6.8	92
SD	3.28	2.69	2.97	0.91	0.96	0.95	0.83	9.15
Min	105	54	57	29.5	53.8	28.5	0.5	72.0
Max	124	69	72	33.7	58.1	32.2	7.9	108.0
n	76	76	74	76	33	76	75	55

## Females: adult

Mean	110	59	60	30.0	55.1	30.1	7.1	82
SD	3.26	2.52	3.70	1.11	0.96	1.09	0.35	10.48
Min	104	53.9	53	26.5	53.2	26.4	6.0	62.0
Max	125	66	69	33.4	57.3	32.7	7.9	113.0
n	108	107	85	108	50	107	106	67

TABLE 35. Measurements (mm) and weights (g) of specimens of *Cicinnurus respublica*

	Wing length	Tail length	Toe central length	Tarsus length	Total head length	Bill length	Bill width	Weight
Males: adult								
Mean	98	39	140	27.1	49.0	25.4	4.1	61
SD	1.49	1.40	6.41	0.55	0.62	1.00	0.32	7.36
Min	94	35	121	25.9	48.0	23.3	3.4	53.2
Max	101	41	150	28	50.2	27.7	5.0	69.0
n	28	28	22	27	13	27	27	6
subadult								
Mean	100	48	81	27.4	50.6	26.5	4.3	59
SD	1.33	4.75	38.22	1.18	2.97	1.27	0.34	
Min	98	41	53	24.6	48.5	25.0	3.7	
Max	102	53	146	28.5	52.7	28.7	4.6	
n	9	9	8	8	2	8	7	1
immature								
Mean	101	52	52	27.8	49.8	26.1	4.5	63
SD	1.34	2.55	1.52	1.06	0.66	0.80	0.07	2.08
Min	99	50	51	26.9	49.0	25.1	4.4	61.1
Max	102	56	54	29.6	50.6	27.2	4.6	65.5
n	5	5	5	5	4	5	5	
Females: adult								
Mean	97	53	52	26.5	49.7	25.5	4.8	56
SD	2.50	2.29	2.24	1.05	1.18	1.42	0.21	3.27
Min	93	49	49	24.7	47.4	22.5	4.5	50.2
Max	101	58	59	28.7	51.6	27.6	5.1	65.5
n	16	16	16	15	9	14	13	7

TABLE 36. Measurements (mm) and weights (g) of specimens of *Paradoxaea raggiana*

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<i>P. raggiana</i>								
Males: adult								
Mean	189	136	447	42.1	69.8	39.6	10.1	272
SD	3.53	4.64	45.31	2.25	0.93	1.11	0.61	16.47
Min	185	128	358	38.6	68.4	37.9	9.3	238
Max	197	144	493	45.6	70.9	41.4	11.1	285
n	9	9	9	8	7	9	9	7
subadult								
Mean	190	139	291	42.2	69.00	38.70	10.23	272
SD	3.61	6.11	206.48	2.38	1.13	1.05	0.21	12.02
Min	186	132	145	39.5	68.2	37.7	10.0	263
Max	193	144	437	43.8	69.8	39.8	10.4	280
n	3	3	2	3	2	3	3	2
immature								
Mean	186	132	126	43.6	69.7	40.4	9.6	233
SD	3.54	4.95	1.41	0.71	0.78	1.20	0.85	10.6
Min	183	128	125	43.1	69.1	39.5	9.0	215
Max	188	136	127	44.1	70.2	41.2	10.2	240
n	2	2	2	2	2	2	2	2
Females: adult								
Mean	164	121	114	38.3	66.9	36.5	9.3	184
SD	5.94	4.39	7.87	1.57	1.03	1.38	0.68	17.82
Min	157	115	103	36.7	65.7	35.2	8.6	170
Max	172	125	125	40.6	68.2	38.3	10.2	215
n	5	5	5	5	4	4	5	5
<i>P. r. augustaevicinae</i>								
Males: adult								
Mean	184	131	451	41.9	66.4	37.5	11.2	276
SD	5.35	3.14	30.12	1.47	1.77	1.13	0.74	24.07
Min	170	124	373	39.4	62.2	35.4	10.0	234
Max	194	136	523	45.5	70.3	39.8	13.0	300
n	37	37	36	37	31	36	37	16
subadult								
Mean	186	131	157	42.6	66.7	37.9	11.4	
SD	3.90	3.57	43.14	1.50	1.36	0.85	0.77	
Min	177	127	119	40.8	64.6	37.0	10.3	
Max	192	139	227	44.6	68.1	39.6	12.8	
n	9	9	9	9	6	9	9	
immature								
Mean	177	129	119	42.4	66.2	37.6	10.8	223
SD	7.11	6.36	7.66	1.41	1.65	1.12	0.58	40.99
Min	163	120	104	39.3	63.5	36.1	9.7	199
Max	191	146	137	45	68.4	39.8	11.4	270
n	15	15	15	15	15	15	15	3
Females: adult								
Mean	161	117	108	38.1	64.2	36.2	10.1	159
SD	8.06	4.91	5.24	2.53	1.35	0.88	0.49	21.27
Min	150	108	100	33.9	62.6	34.8	9.2	133
Max	180	126	120	44	67.8	37.8	10.9	195
n	27	27	26	26	15	27	27	10
<i>P. r. intermedia</i>								
Males: adult								
Mean	185	132	448	42.4	68.2	39.1	10.5	257
SD	4.02	3.85	34.43	2.00	2.53	1.13	0.60	20.82
Min	178	127	384	39	64.5	36.4	9.0	234
Max	191	141	505	45.7	71.2	40.6	11.5	274
n	18	18	15	18	7	15	16	3
subadult								
Mean	186	131	325	41.8	69.0	39.7	10.4	
SD	4.49	3.29	125.82	1.38	0.66	1.69	0.54	
Min	180	127	130	39.6	68.4	37.8	9.7	
Max	190	136	440	43.1	69.7	42.2	11.1	
n	5	5	5	5	3	5	5	
<i>immature</i>								
Mean	175	128	121	43.0	64.4	38.6	10.2	225
SD	4.03	3.77	5.48	1.22		1.38	1.17	
Min	172	124	117	41.4		37.0	9.3	
Max	181	133	129	44.1		39.6	11.5	
n	4	4	4	4	1	3	3	1
<i>Females: adult</i>								
Mean	162	121	114	37.6	65.3	37.3	9.7	192
SD	8.08	5.85	6.17	2.50	1.71	1.19	0.72	40.31
Min	148	112	104	35.4	62.0	35.5	8.6	163
Max	178	128	126	41.2	68.4	37.3	10.9	220
n	13	13	13	12	10	13	13	2
<i>P. r. salvadori</i>								
Males: adult								
Mean	188	135	463	43.0	69.9	38.9	9.8	266
SD	4.47	5.53	31.06	1.35	1.31	1.17	0.48	15.25
Min	180	125	410	38.8	67.0	36.5	9.0	240
Max	198	154	527	45.6	72.5	41.1	10.8	295
n	41	42	38	42	23	42	42	21
subadult								
Mean	186	133	284	43.5	69.0	38.8	9.8	249
SD	5.30	5.89	146.12	1.52	0.98	1.09	0.53	26.24
Min	178	122	115	40.3	67.6	36.7	8.8	210
Max	197	143	517	46.3	71.0	40.5	10.7	288
n	20	20	17	19	13	20	18	9
immature								
Mean	177	127	120	42.7	69.1	38.7	9.7	225
SD	7.51	6.07	7.19	1.99	1.81	1.40	0.69	23.54
Min	160	115	106	35.4	66.3	36.4	8.6	189
Max	190	136	131	45.1	71.6	42.1	11.2	255
n	23	23	22	22	11	23	23	8
<i>Females: adult</i>								
Mean	164	120	111	37.5	66.3	37.4	9.6	175
SD	6.42	5.15	6.66	1.39	1.48	1.04	0.46	17.59
Min	150	110	100	34.1	63.9	34.9	8.7	135
Max	182	132	128	40.3	69.8	40.4	10.4	210
n	31	31	29	30	20	31	31	24
<i>oil subspecies</i>								
Males: adult								
Mean	186	133	455	42.4	68.1	38.5	10.4	270
SD	4.90	4.83	32.85	1.65	2.30	1.36	0.88	19.38
Min	160	124	358	38.6	62.2	35.4	9.0	234
Max	198	154	527	45.7	72.5	41.4	13.0	300
n	105	106	98	106	68	102	104	47
subadult								
Mean	186	133	256	42.9	68.4	38.7	10.3	253.5
SD	4.72	5.31	146.88	1.60	1.45	1.25	0.88	25.40
Min	178	122	115	39.5	64.6	36.7	8.8	210
Max	197	144	517	46.3	71.0	42.2	12.8	288
n	37	37	33	36	24	37	35	11
immature								
Mean	177	128	120	42.6	67.5	38.4	10.1	225
SD	7.10	5.84	7.07	1.69	2.26	1.42	0.87	23.99
Min	160	115	106	35.4	63.5	36.1	8.6	189
Max	191	146	137	45.1	71.6	42.1	11.5	270
n	44	44	43	43	29	43	40	14
Females: adult								
Mean	162	119	111	37.8	65.5	36.9	9.8	173
SD	7.26	5.27	6.44	2.05	1.73	1.17	0.58	20.79
Min	148	108	100	33.9	62.0	34.8	8.6	133
Max	182	132	128	44.2	69.8	40.4	10.9	220
n	76	76	73	73	49	75	76	41



TABLE 37. Measurements (mm) and weights (g) of specimens of *Paradisaea apoda*

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<i>P. a. apoda</i>								
<b>Males: adult</b>								
Mean	232	165	637	52.6	77.3	43.9	9.6	
SD	4.61	5.11	104.72	2.42	3.05	2.77	0.55	
Min	225	156	500	45.0	71.5	37.7	8.1	
Max	240	175	854	54.8	80	47.6	10.4	
n	16	16	14	17	6	16	17	
<b>subadult</b>								
Mean	228	161	361	52.3	76.0	44.4	9.65	
SD	5.25	5.33	205.60	1.44	1.55	1.58	0.27	
Min	219	152	150	49.6	74.7	42.6	9.2	
Max	239	170	659	54.6	77.9	48.0	10.2	
n	12	12	11	12	4	12	12	
<b>immature</b>								
Mean	209	151	146	51.2	75.9	44.0	9.6	
SD	9.07	5.68	8.61	2.71	3.98	2.23	0.49	
Min	198	141	132	45.0	72.5	41.4	8.9	
Max	224	161	160	53.4	80.3	48	10.3	
n	8	8	8	8	3	8	8	
<b>Females: adult</b>								
Mean	202	152	144	48.6	73.7	42.6	9.5	
SD	6.73	5.76	7.23	3.77	2.36	1.84	0.45	
Min	194	141	132	44.9	71.4	40.1	8.9	
Max	215	158	153	53.2	77.7	45.1	10.2	
n	8	8	8	8	7	8	8	
<i>P. a. novaeguineae</i>								
<b>Males: adult</b>								
Mean	206	146	591	46.7	72.5	40.4	9.4	
SD	3.05	3.95	57.60	1.20	1.27	1.25	0.32	
Min	200	140	480	44.6	70.0	37.6	9.0	
Max	213	154	663	48.9	74.7	42.6	10.1	
n	24	22	17	24	9	22	23	
<b>subadult</b>								
Mean	203	143	356	46.17	70.9	40.1	9.27	
SD	4.44	3.66	217.40	1.02	1.64	0.99	0.40	
Min	190	135	134	44.8	68.8	38.8	8.6	
Max	210	148	662	48.9	73.3	43.0	10.1	
n	27	26	19	26	7	24	26	
<b>immature</b>								
Mean	191	137	135	47.0	71.0	40.1	9.3	224
SD	7.95	3.90	6.77	1.21	2.27	0.95	0.35	2.12
Min	180	130	125	44.8	65.5	38.1	8.7	222
Max	209	143	146	49.3	74.0	41.6	10.1	225
n	25	24	21	25	14	22	25	2
<b>Females: adult</b>								
Mean	173	128	119	40.9	68.0	39.0	8.9	172
SD	6.29	6.76	6.84	1.88	1.04	1.09	0.36	2.12
Min	159	118	105	38.8	66.6	37.1	8.2	170
Max	188	142	132	45.8	70.5	40.7	9.6	173
n	26	26	25	26	15	25	25	2
<b>all subspecies</b>								
<b>Males: adult</b>								
Mean	217	154	612	49.1	74.4	41.9	9.5	
SD	13.39	10.44	84.10	3.43	3.20	2.65	0.43	
Min	200	140	480	44.6	70.0	37.6	8.1	
Max	240	175	854	54.8	80.0	47.6	10.4	
n	40	38	31	41	15	38	40	
<b>subadult</b>								
Mean	211	148	358	48.092	72.76	41.51	9.39	
SD	12.50	9.56	209.6	3.10	3.00	2.39	0.41	
Min	190	135	134	44.8	68.8	38.8	8.6	
Max	239	170	662	54.6	77.9	48.0	10.2	
n	39	38	30	38	11	36	38	

<b>immature</b>								
Mean	196	140	138	48.0	71.9	41.2	9.3	224
SD	11.19	7.71	8.56	2.46	3.15	2.23	0.41	2.12
Min	180	130	125	44.8	65.5	38.1	8.7	2.2
Max	224	161	160	53.4	80.3	48.0	10.3	2.25
n	33	32	29	33	17	30	33	2
<b>Females: adult</b>								
Mean	180	133	125	42.7	69.8	39.9	9.1	172
SD	13.92	12.23	12.52	4.11	3.11	2.01	0.46	2.12
Min	159	118	105	38.8	66.6	37.1	8.2	170
Max	215	158	153	53.2	77.7	45.1	10.2	173
n	34	34	33	34	22	33	33	2

TABLE 38. Measurements (mm) and weights (g) of specimens of *Paradisaea minor*

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<i>P. m. minor</i>								
<b>Males: adult</b>								
Mean	188	127	503	44.7	69.5	39.0	10.5	239
SD	4.71	4.43	48.76	1.65	2.19	1.70	0.45	23.72
Min	180	116	420	39.4	65.3	34.0	9.2	185
Max	196	133	641	47.8	72.5	42.5	11.4	285
n	27	27	23	27	19	27	27	12
<b>subadult</b>								
Mean	184	125	318	44.1	68.7	37.8	10.4	
SD	5.62	4.57	155.64	1.72	1.97	1.68	0.43	
Min	172	115	108	39.5	64.9	34.5	9.7	
Max	195	132	498	46.5	71.5	40.8	11.2	
n	21	20	16	19	14	21	21	
<b>immature</b>								
Mean	179	123	116	43.8	68.3	38.1	10.3	216
SD	8.00	6.27	7.57	2.20	1.96	1.57	0.65	19.91
Min	162	105	98	39.2	64.8	36.0	9.3	186
Max	194	130	127	46.9	72.7	41.4	12.1	242
n	22	22	18	21	21	22	22	7
<b>Females: adult</b>								
Mean	161	112	103	39.7	65.8	37.0	10.0	158
SD	6.18	6.06	6.50	2.30	1.70	1.42	0.68	10.84
Min	152	103	93	37.1	62.8	34.7	9.0	145
Max	174	126	118	45.2	69.0	40.0	11.7	170
n	23	22	19	23	21	23	22	6
<i>P. m. finschi</i>								
<b>Males: adult</b>								
Mean	190	131	469	44.4	70.0	38.3	10.4	256
SD	5.47	4.27	23.69	2.32	1.76	1.17	0.78	29.09
Min	180	124	430	39.2	66.8	35.7	8.5	183
Max	199	141	537	49.2	73.8	40.6	11.9	300
n	27	26	24	26	22	27	26	21
<b>subadult</b>								
Mean	190	130	357	44.6	68.8	38.2	10.5	230
SD	4.62	4.95	133.06	1.14	1.51	1.09	0.76	
Min	182	124	133	41.9	66.8	36.1	9.7	
Max	201	141	481	46	71.2	40.3	11.8	
n	15	15	14	15	13	15	15	1
<b>immature</b>								
Mean	179	124	121	43.9	67.8	37.3	9.8	205
SD	8.26	5.34	7.10	2.23	2.05	1.67	0.68	29.42
Min	165	110	108	40.6	62.8	32.2	8.7	151
Max	193	131	131	46.7	70.8	39.1	10.8	268
n	18	16	14	16	11	16	15	14
<b>Females: adult</b>								
Mean	164	115	109	41.4	66.9	37.4	10.2	164
SD	6.45	4.73	8.57	2.97	1.78	1.31	0.58	18.46
Min	152	104	97	36.5	64.3	34.5	9.0	141
Max	175	123	129	47.4	71.3	40.7	11.4	210
n	26	26	24	25	22	26	26	16

<i>P. m. jobiensis</i>								
<b>Males: adult</b>								
Mean	200	137	495	48.2	71.0	39.4	10.8	298
SD	7.55	3.78	62.64	1.15	2.69	1.31	0.52	4.04
Min	183	130	353	45.5	67.4	36.8	9.6	293
Max	210	144	566	49.4	73.6	41.4	11.5	300
n	12	12	9	11	7	10	12	3
<b>subadult</b>								
Mean	196	135	349	48.3	71.2	39.8	10.5	240
SD	5.75	6.50	145.88	2.09	2.00	1.48	1.00	
Min	184	122	162	43.9	68.5	37.5	9.2	
Max	203	143	482	50.1	73.7	42	12.5	
n	9	9	7	9	6	9	9	1
<b>immature</b>								
Mean	189	131	122	47.3	71.2	39.7	10.9	230
SD	12.19	4.53	6.40	1.97	1.26	0.77	0.71	28.28
Min	163	124	114	43.0	69.3	38.8	10.1	210
Max	200	138	130	49.0	72.8	40.7	12.2	250
n	8	8	8	8	7	8	8	2
<b>females: adult</b>								
Mean	172	121	112	42.2		36.4	9.4	175
SD								20.31
Min								152
Max								189
n	1	1	1	1		1	1	3
<i>P. m. pulchra</i>								
<b>Males: subadult</b>								
Mean	190	130	435	45.1	66.8	38.3	10.8	
SD	4.65	4.03	29.74	1.95		0.99	0.28	
Min	184	124	403	43.7		36.9	10.5	
Max	194	133	462	47.3		39.0	11.1	
n	4	4	3	3	1	4	4	
<b>immature</b>								
Mean	187	128	121	44.9	71.7	40.5	10.3	
n	1	1	1	1	1	1	1	
<b>Females: adult</b>								
Mean	160	112	101	39.1	68.1	39.2	10.2	186
SD	2.45	0.96	4.32	0.29	0.35	0.60	0.52	
Min	157	111	95	38.9	67.8	38.6	9.4	
Max	162	113	105	39.5	68.3	40	10.5	
n	4	4	4	4	2	4	4	1

<i>all subspecies</i>								
<b>Males: adult</b>								
Mean	191	130	487	45.2	70.0	38.8	10.5	254
SD	6.91	5.49	44.93	2.32	2.00	1.47	0.62	30.13
Min	180	116	353	39.2	65.3	34.0	8.5	183
Max	210	144	641	49.4	73.8	42.5	11.9	300
n	66	65	56	64	43	64	65	36
<b>subadult</b>								
Mean	189	129	346	45.1	69.1	38.3	10.5	235
SD	6.70	6.02	139.79	2.28	2.01	1.56	0.66	7.07
Min	172	115	108	39.5	64.9	34.5	9.2	230
Max	203	143	498	50.1	73.7	42.0	12.5	240
n	50	48	40	46	34	49	49	2
<b>immature</b>								
Mean	181	125	119	44.4	68.7	38.1	10.2	210
SD	9.52	6.33	7.30	2.45	2.23	1.69	0.71	26.82
Min	162	105	98	39.2	62.8	32.2	8.7	151
Max	200	138	131	49.0	72.8	41.4	12.2	268
n	51	50	44	48	42	50	49	23
<b>Females: adult</b>								
Mean	163	114	106	40.4	66.3	37.2	10.1	165
SD	6.36	5.49	7.96	2.67	1.83	1.44	0.61	17.47
Min	152	103	93	36.5	62.8	34.5	9.0	141
Max	175	126	129	47.4	71.3	40.7	11.7	210
n	56	55	50	55	47	56	55	26

TABLE 39. Measurements (mm) and weights (g) of specimens of *Paradisaea decora*

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<b>Males: adult</b>								
Mean	181	137	431	41.1	67.6	36.7	8.9	237
SD	2.62	3.47	41.70	0.96	2.13	1.03	0.47	
Min	177	128	368	39.0	64.1	35.2	8.2	
Max	185	143	536	42.5	70.9	40.0	9.8	
n	22	22	16	21	7	20	20	1
<b>subadult</b>								
Mean	180	139	290	41.4	66.9	36.8	8.9	
SD	2.32	1.97	94.49	0.59	0.77	0.93	0.51	
Min	176	136	177	40.4	65.7	34.5	8.2	
Max	185	142	448	42.3	68.1	38.3	9.9	
n	17	17	16	16	7	17	16	
<b>immature</b>								
Mean	172	138	120	41.2	65.9	36.6	9.1	
SD	5.11	3.79	2.73	0.74		1.04	0.23	
Min	164	134	116	40.2		35.1	8.8	
Max	178	144	123	42.2		37.8	9.4	
n	7	7	6	7	1	6	7	
<b>Females: adult</b>								
Mean	160	128	109	37.2	64.5	35.9	8.9	
SD	2.56	2.82	2.27	0.79	0.40	1.31	0.48	
Min	157	123	104	36.4	64.1	34.4	7.9	
Max	165	131	112	38.5	64.9	38.7	9.6	
n	8	8	8	8	3	8	8	

TABLE 40. Measurements (mm) and weights (g) of specimens of *Paradisaea rubra*

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<b>Males: adult</b>								
Mean	176	119	563	41.9	63.9	35.5	8.6	201
SD	3.72	2.72	60.89	1.41	1.28	1.86	0.68	25.62
Min	169	114	478	37.6	60.8	30.9	7.0	158
Max	186	125	765	43.7	65.7	39.2	9.7	224
n	27	27	23	26	18	26	27	7
<b>subadult</b>								
Mean	174	121	243	41.7	63.1	34.0	8.2	201
SD	3.07	3.00	107.47	0.79	1.15	1.00	0.38	
Min	168	115	112	40.5	61.2	32.0	7.5	
Max	178	125	457	43.4	64.5	36.2	9.0	
n	17	17	16	17	7	17	16	1
<b>immature</b>								
Mean	170	119	117	42.3	63.4	35.2	8.6	195
SD	4.43	4.19	5.22	1.29	1.56	1.52	0.49	
Min	162	112	109	40.3	61.0	33.3	7.6	156
Max	178	126	127	44.7	65.8	38.4	9.2	212
n	10	10	9	10	7	10	10	8
<b>Females: adult</b>								
Mean	159	114	106	38.8	63.1	34.6	8.5	158
SD	6.26	4.19	3.88	1.84	1.61	1.28	0.62	26.83
Min	151	105	102	36.2	60.2	32.8	7.1	115
Max	174	121	117	43.5	66.4	38.5	9.8	208
n	26	26	24	25	12	26	26	1

TABLE 41. Measurements (mm) and weights (g) of specimens of *Paradisaea guilhelmi*

	Wing length	Tail length	Tail central length	Tarsus length	Head length	Bill length	Bill width	Weight
<b>Males: adult</b>								
Mean	177	114	557	44.5	72.5	40.9	8.9	256
SD	3.69	3.58	75.41	1.18	1.48	1.65	0.43	6.74
Min	172	107	498	44.4	69.0	36.6	8.1	250
Max	188	121	600	46.0	76.0	43.3	9.7	265
n	27	27	27	27	27	27	27	27
<b>subadult</b>								
Mean	177	116	168	44.3	73.5	41.8	9.3	250
SD	2.78	2.95	24.21	1.18	1.41	1.17	0.63	
Min	173	112	110	44.0	70.0	40.4	8.6	
Max	182	121	427	46.0	76.0	43.5	10.7	
n	10	10	10	10	10	10	9	1
<b>immature</b>								
Mean	172	117	114	44.1	74.2	43.3	9.6	219
SD	6.61	6.61	6.61	1.22	2.01	1.61	0.28	43.8
Min	163	113	104	44.0	70.0	42.3	9.3	188
Max	179	120	120	46.0	76.0	45.7	9.9	250
n	4	3	4	4	3	4	4	2
<b>Females: adult</b>								
Mean	158	106	104	40.3	70.3	39.9	9.0	
SD	5.82	3.27	6.24	1.15	1.46	1.09	0.52	
Min	151	101	98	39.8	68.0	37.6	8.0	
Max	171	117	111	40.8	73.2	42	10.0	
n	15	15	15	15	15	15	15	

TABLE 42. Measurements (mm) and weights (g) of specimens of *Paradisaea rudolphi*

	Wing length	Tail length	Tail central length	Tarsus length	Head length	Bill length	Bill width	Weight
<b><i>P. r. rudolphi</i></b>								
<b>Males: adult</b>								
Mean	157	83	409	40.1	70.7	41.6	8.6	177
SD	2.72	4.06	24.19	1.30	1.44	1.56	0.57	2.12
Min	153	76	341	36.5	68.2	39.6	7.6	175
Max	163	91	452	41.8	74.8	45.6	9.6	178
n	20	20	17	19	19	19	20	2
<b>subadult</b>								
Mean	160	87	102	39	70.9	42.3	8.45	
SD	4.24	3.54	0.71	0.99	0.79	0.71	0.49	
Min	157	84	101	38.3	70.3	41.8	8.1	
Max	163	89	102	39.7	71.4	42.8	8.8	
n	2	2	2	2	2	2	2	
<b>immature</b>								
Mean	155	93	96	40.0	70.1	41.3	8.4	165
SD	3.30	3.16	4.50	1.14	1.00	0.41	0.19	
Min	150	90	91	38.8	70.1	40.9	8.3	
Max	157	97	102	41.2	71.4	41.8	8.7	
n	4	4	4	4	4	4	4	1
<b>Females: adult</b>								
Mean	150	95	95	38.4	69.2	40.8	8.6	157
SD	5.71	4.24	3.46	1.68	1.66	1.18	0.47	
Min	142	90	90	35.5	68.4	38.4	8.0	
Max	158	102	101	41.0	71.4	42.9	9.7	
n	15	15	14	15	13	14	15	1

<b><i>P. r. ampla</i></b>								
<b>Males: adult</b>								
Mean	154	82	409	38.1	68.4	39.7	8.2	178
SD	3.27	3.21	12.06	1.70	0.88	0.68	0.39	5.56
Min	151	78	378	36.1	67.5	39.0	7.6	174
Max	159	86	422	40.1	69.7	40.4	8.5	189
n	5	5	3	5	5	5	5	6
<b>immature</b>								
Mean	152	93	94	38.4	68.7	40.3	8.4	163
SD	5.15	3.08	2.66	1.55	1.18	0.85	0.45	10.34
Min	142	90	90	35.7	66.9	39.2	7.7	149
Max	157	99	98	40.6	70	41.8	9.1	174
n	7	7	6	7	6	7	7	4
<b>Female</b>								
Mean	147	91	94	36.3	65.3	38.0	8.2	
n	1	1	1	1	1	1	1	
<b><i>P. r. margaritae</i></b>								
<b>Males: adult</b>								
Mean	156	78	451	37.8	69.4	41.3	8.8	158
SD	2.95	1.87	12.70	0.82	1.51	1.35	0.54	
Min	151	76	436	36.6	68.0	39.3	8.1	
Max	158	81	458	38.9	71.0	42.3	9.6	
n	5	5	3	5	3	4	5	1
<b>immature</b>								
Mean	156	98	97	39.1	69.2	40.1	8.4	169
SD	3.71	2.39	1.82	1.14	1.70	1.42	0.39	4.24
Min	151	95	95	37.7	68.0	38.6	7.9	166
Max	161	101	100	40.4	70.4	42	8.9	172
n	5	5	5	4	2	5	5	2
<b>Females: adult</b>								
Mean	148	89	92	37.4	68.1	40.3	8.8	152
SD	5.22	2.70	3.44	1.38	1.49	1.24	0.29	23.97
Min	143	86	88	35.7	66	38.4	8.5	124
Max	159	94	96	39.5	70	41.9	9.2	166
n	7	7	6	7	6	7	7	3
<b>all subspecies</b>								
<b>Males: adult</b>								
Mean	157	82	414	39.4	70.1	41.2	8.6	176
SD	3.06	3.95	25.67	1.65	1.62	1.56	0.56	7.99
Min	151	76	341	36.1	67.5	39.0	7.6	158
Max	163	91	458	41.8	73.8	45.6	9.6	189
n	30	30	23	29	24	28	30	9
<b>subadult</b>								
Mean	160	87	102	39	70.9	42.3	8.5	
SD	4.24	3.54	0.71	0.99	0.78	0.71	0.49	
Min	157	84	101	38.3	70.3	41.8	8.1	
Max	163	89	102	39.7	71.4	42.8	8.8	
n	2	2	2	2	2	2	2	
<b>immature</b>								
Mean	154	95	96	39.0	69.1	40.5	8.4	165
SD	4.36	3.52	3.31	1.41	1.20	1.04	0.36	8.1
Min	142	90	90	35.7	66.9	38.6	7.7	149
Max	161	101	102	41.2	70.4	42.0	9.1	174
n	16	16	15	15	10	16	16	7
<b>Females: adult</b>								
Mean	149	93	94	38.0	68.7	40.5	8.7	153
SD	5.39	4.52	3.64	1.63	1.80	1.29	0.43	19.75
Min	142	86	88	35.5	65.3	38.0	8.0	124
Max	159	102	101	41.0	72.0	42.9	9.7	166
n	23	23	21	23	20	22	23	4

**NEW DISTRIBUTION AND HABITAT DATA FOR THE PYGOPODID, *PARADELMA ORIENTALIS* (GÜNTHER, 1876).** *Memoirs of the Queensland Museum* 42(1): 212. 1997:- Four specimens of *Paradelma orientalis* (QM transparency NR221-3) collected recently (4 Sept., 1996) in Eena State Forest (28°19'S 150°50'E) 20km WNW of Inglewood, SCQ extend the knowledge of the distribution and habitat preferences of this species. This locality is approximately 110km south of Dunmore State Forest, near Cecil Plains, SCQ (26°24'S, 151°01'E), the former southernmost known collection locality for the species (S. Wilson, QM, pers. comm.). The specimens were unremarkable morphologically, closely resembling the photographs in Cogger (1996) and Wilson & Knowles (1988). Snout-vent lengths were 154, 155, 156 and 172mm.

In Eena State Forest, three specimens were collected in *Eucalyptus crebra* and *E. microcarpa* open forest with a dense subcanopy dominated by *Callitris columellaris* and *Allocasuarina luehmannii* on loose sandy clay substrate at 28°19'S 150°50'E. The site had been silviculturally treated on three occasions between 1937 and 1973 and sections logged in 1971 (Inglewood DPI Forestry records). The remaining specimen was found in *A. luehmannii* closed forest with widely scattered *E. crebra* emergents on a similar substrate at 28°21'S 150°50'E. This site had been silviculturally treated in the 1930s and 1950s and partially logged in 1984 (Inglewood DPI Forestry records). In both sites, all individuals were found sheltering under thick slabs of *E. crebra* bark that had fallen from standing ringbarked trees.

*P. orientalis* is one of several species of reptiles from Queensland's Brigalow Biogeographic Region with special conservation 'rating'. It is treated as 'vulnerable' by McDonald et al., 1991; Cogger et al., 1993 and Queensland Nature Conservation Regulation 1994. Little is known about the species' biology and habitat preferences (Kluge, 1974; Jenkins, 1979; Shea, 1987; Cogger et al., 1993; Cogger, 1996). Previous published records suggested the species was confined to remnant *Acacia harpophylla* forest and eucalypt woodland with an understorey of *A. harpophylla* or sparse tussock grass ground vegetation on grey cracking soils (e.g., Shea, 1987; Cogger et al., 1993).

This range extension combined with the knowledge that *P. orientalis* appears to adapt to several soil and vegetation types indicate that the species is more widespread than supposed. Further, these records combined with recent observations in *Acacia falciformis* woodland on Boyne Island (23°50'S 150°24'E) (M. Fitzgerald, pers. comm.); on a sandstone rise in dry sclerophyll forest in Dunmore State Forest (S. Wilson, pers. comm.); in *Corymbia maculata* and *E. crebra* dominated open forest in Barakula State Forest (26°17'S 150°52'E) (D.

Hannah, pers. comm.); and in mixed species open woodland with *Triodia mitchelli* dominated ground layer in the Chesteron Range, Charleville district (26°09'S 147°14'E) (C. Dollery, pers. comm.) suggest it may be more abundant than the published records indicate.

Whether the conservation status of *P. orientalis* should be modified requires further investigation.

### Acknowledgements

Thanks are due to Maritza de Oliveira for assisting with fieldwork; Dave Hannah for providing details on the Barakula record; Col Dollery for providing details on the Chesteron Range records; Steve Wilson for providing details on his southernmost localities for the species; and Mark Fitzgerald for providing valuable comments about the species and taking photographs that are lodged with the QM. Jeanette Covacevich, Mark Fitzgerald and Geoff Smith commented on early drafts of this note. The work was conducted as part of the Dept of Natural Resources research into the distribution and habitat requirements of fauna occurring in production forests in Queensland.

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## NOTES ON THE GENUS *THORELLIOLA* STRAND, 1942 (ARANEAE: SALTICIDAE)

JOANNA GARDZINSKA AND BARBARA PATOLETA

Gardzinska, J. & Patoleta, B. 1997 06 30: Notes on the genus *Thorelliola* Strand, 1942 (Araneae: Salticidae). *Memoirs of the Queensland Museum* 42(1): 213-222. Brisbane. ISSN 0079-8835.

Genus *Thorelliola* Thorell, 1887 is studied. Five species are diagnosed, described and illustrated. Four of them, *T. biapophysis*, *T. glabra*, *T. javaensis*, *T. truncilonga*, are described as the new. Remarks on relationships and distribution are presented. □ *Thorelliola*, Indonesia, Papua New Guinea, Tahiti.

Gardzinska, J. & Patoleta, B., Zakład Zoologii WSR-P, Prusa 12, 08-110 Siedlce, Poland; 18 February 1997.

Genus *Thorelliola* was established by Strand (1942) for *Thorellia ensifera* (Thorell). The type species was originally described as *Plexippus ensifer* Thorell, 1877 and then transferred into *Thorellia* by Keyserling (1882). The latter generic name was, however, preoccupied, thus *Thorelliola* is the present valid name. Simon (1901) included the genus (*Thorellia* at that time) into a group *Spilargeae* — together with *Eupalia* and *Spilargis*. Petrunkevich (1928) added six other genera, none of them related. According to Berry, Beatty & Prószyński (in prep.), body shape and genitalia structures of *Thorelliola* resemble *Euophrys* and related genera.

Males of *Thorelliola* are very distinctive for their 'horns' arising either from circular sockets on the clypeus or from a tip of a robust truncus. Such strange and extravagant structures are also found in genera *Padilla* Simon, *Allococalodes* Wanless and *Cocalodes* Pocock. According to Wanless & Lubin (1986) the structures are probably used during intra-specific ♂-♂ interactions. The same authors suggest that the horns in *Thorelliola* have evolved from the lower of two setae, that form part of a triad of stiff setae on the clypeus in many salticids. The function of the horns in *Thorelliola* seems still unknown. Since there are no pores on any part of them, they cannot be used for dispersing pheromones, moreover, there is no evidence of any spider being injured by horns of another spider (Jackson & Whitehouse, 1982), so these structures cannot be the weapons. Zabka (1988) suggests that the protruding spines may work as stridulatory organs together with the corresponding palpal spines.

### MATERIAL AND METHODS

Material from Indonesia and Tahiti, from Dr C.L. Deeleman-Reinhold's collection and speci-

mens collected by D.J. Court from Papua New Guinea are deposited in the Queensland Museum, Brisbane (QM). Comparative material from Singapore and Sulawesi (Indonesia) was borrowed from the Naturhistoriska Riksmuseet, Stockholm (NRS). Measurements are given in millimetres. The drawings were made using a grid system. Dissected epigynes were digested in lactic acid. Abbreviations used are: AEW = anterior eye row width, ag = accessory gland, AL = abdominal length, CH = cephalothorax height, CL = cephalothorax length, CW = cephalothorax width, e = embolus, EFL = eye field length, fd = fertilisation duct, h = horn, id = insemination duct, la = lateral appendix, PEW = posterior eye row width, pta = prolateral tibial apophysis, rta = retrolateral tibial apophysis, s = spermatheca, sd = seminal duct, t = truncus.

Order ARANEAE  
Family SALTICIDAE

### *Thorelliola* Strand, 1942

*Thorellia* Keyserling, 1882: 1353.

*Thorelliola* Strand, 1942: 400; Prószyński, 1984: 148; Zabka, 1988: 470-471; Jackson & Whitehouse, 1989: 1-16; Koh, 1989: 118.

**DIAGNOSIS.** Small spiders (3.5-5.0) with relatively high cephalothorax. Abdomen nearly round; legs rather robust and long (IV the longest). ♂ ♂ with horns or a truncus on the clypeus, in ♀ ♀ two smaller and more delicate setae.

**DESCRIPTION.** Cephalothorax longer than wide. Clypeus low. Cephalothorax usually yellow-beige to brown, posteriorly darker. Abdomen oval, light with grey-black pattern, covered with shiny scales. Chelicerae with two prolateral teeth and one retrolateral fissidentate tooth, with mul-

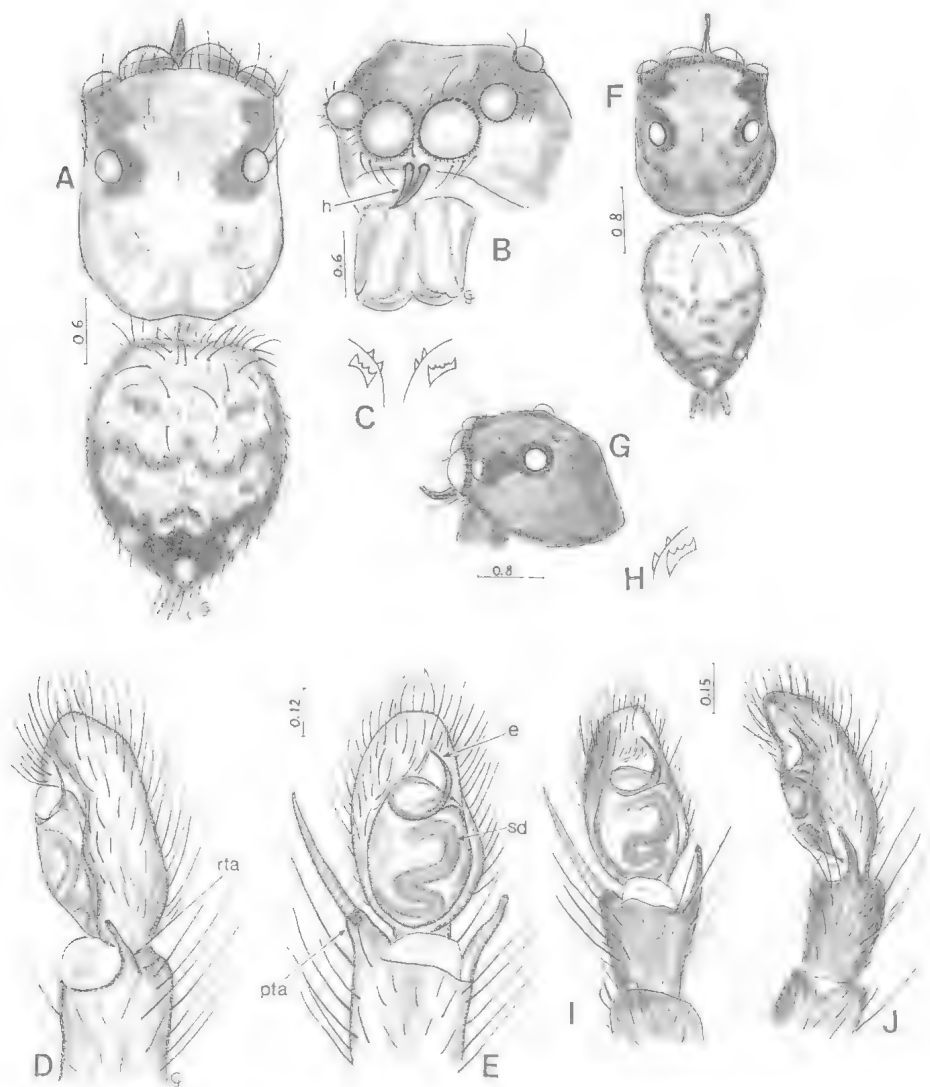


FIG. 1. *Thorelliola ensifera*, ♂♂. A-E, from Bali. F-J, comparative material from Singapore. A-B, F-G, general views. C, H, cheliceral teeth. D-E, I-J, palpal organs (lateral and ventral views).

tiple cusps. External margins of ♂ chelicerae with a lateral cusp. Maxillae and labium not distinctive, sternum heart-shaped. Legs relatively robust and long, yellow-brown with darker markings, especially near the joints. Leg formula: IV, III, I, II. Palpal organ simple, embolus counter-clockwise, weakly sclerotized. Epigyne, transverse oval, spermathecae more or less spherical; insemination ducts rather short, without loops.

**DISTRIBUTION.** Malaysia, Indonesia, Polynesia, Hawaii, Tahiti, Melanesia, Singapore, Papua New Guinea.

***Thorelliola ensifera* (Thorell, 1877)**  
(Figs 1-3)

*Plexippus ensifer* Thorell, 1877: 606.

*Thorellia ensifera* Keyserling, 1882: 1353.

*Thorelliola ensifera* Strand, 1942: 400; Prószyński, 1984: 148; Wanless & Lubin, 1986: 1211, 1214; Zabka, 1988: 470-471; Jackson & Whitehouse, 1989: 1-16; Koh, 1989: 118.

**MATERIAL EXAMINED.** QMS35296, ♂, Bali: Sanur, 5.08.1992., C.L. Deeleman-Reinhold; QMS35297, ♀, North Sulawesi: Dumoga Bone National Park, near Doloduo, 27-30.07.1982; QMS35298, ♀, Tahiti, 1000m, 15.02.1985, C.L. Deeleman-Reinhold. **COMPARATIVE**

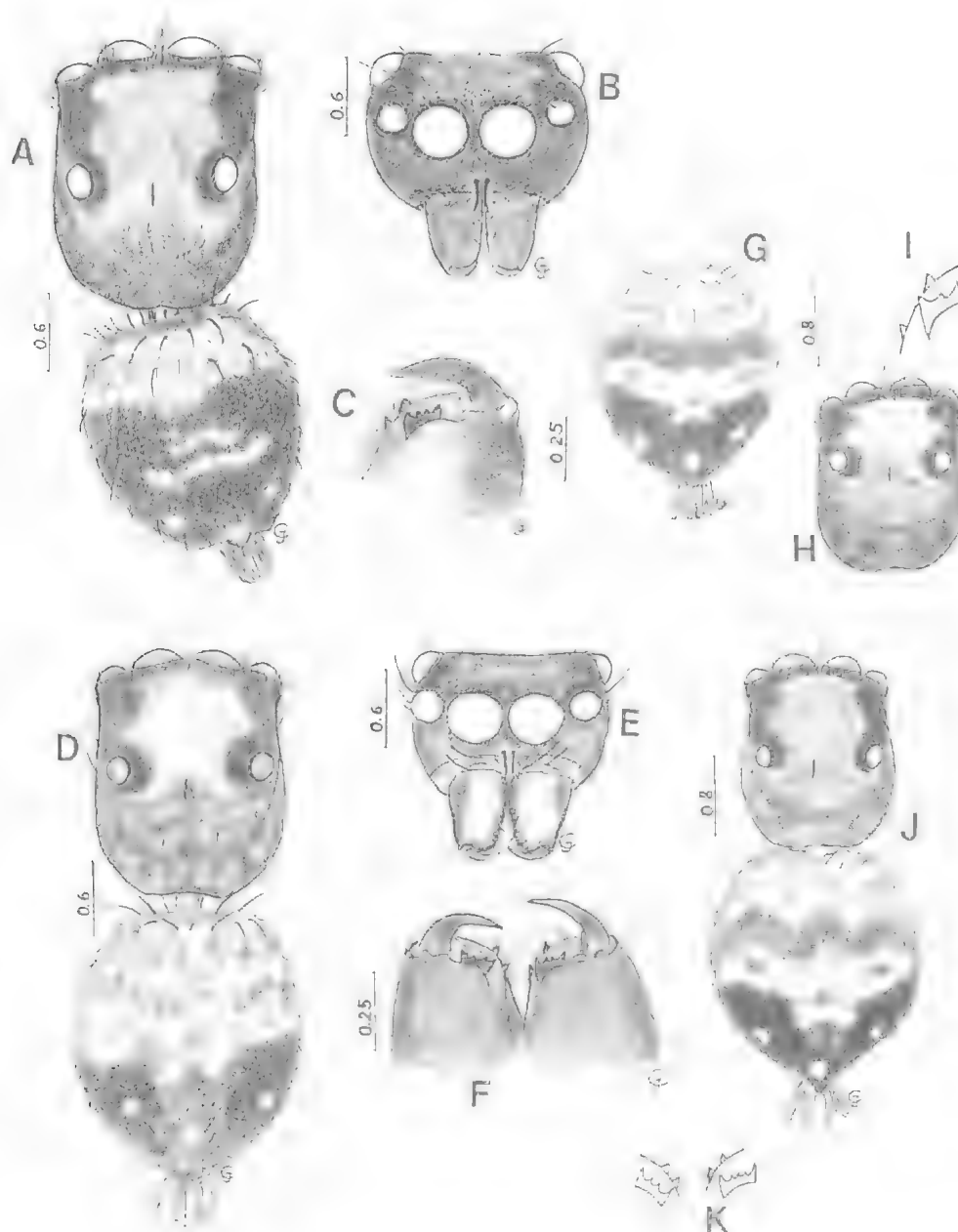


FIG. 2. *Thorelliola ensifera*, ♀♀. A-C, from Sulawesi. D-F, from Tahiti. G-I, comparative material from Sulawesi. J-K, comparative material from Singapore. A-B, D-E, G-H, J, general views. C, F, I, K, cheliceral teeth.

**MATERIAL.** NRS267/1806b, ♂, ♀, Singapore (Workman ded.), Thorell; NRS267/1806a, ♀, Sulawesi (Doria ded.), Thorell.

protruding on the clypeus, and by the shape of embolus and spermathecae. Abdomen with three white posterior spots.

**COMPARISON.** *T. ensifera* differs from the other species by the presence of two central horns

**DESCRIPTION.** Male. Cephalothorax (Fig. 1A-B) moderately tall, yellow-brown, covered with

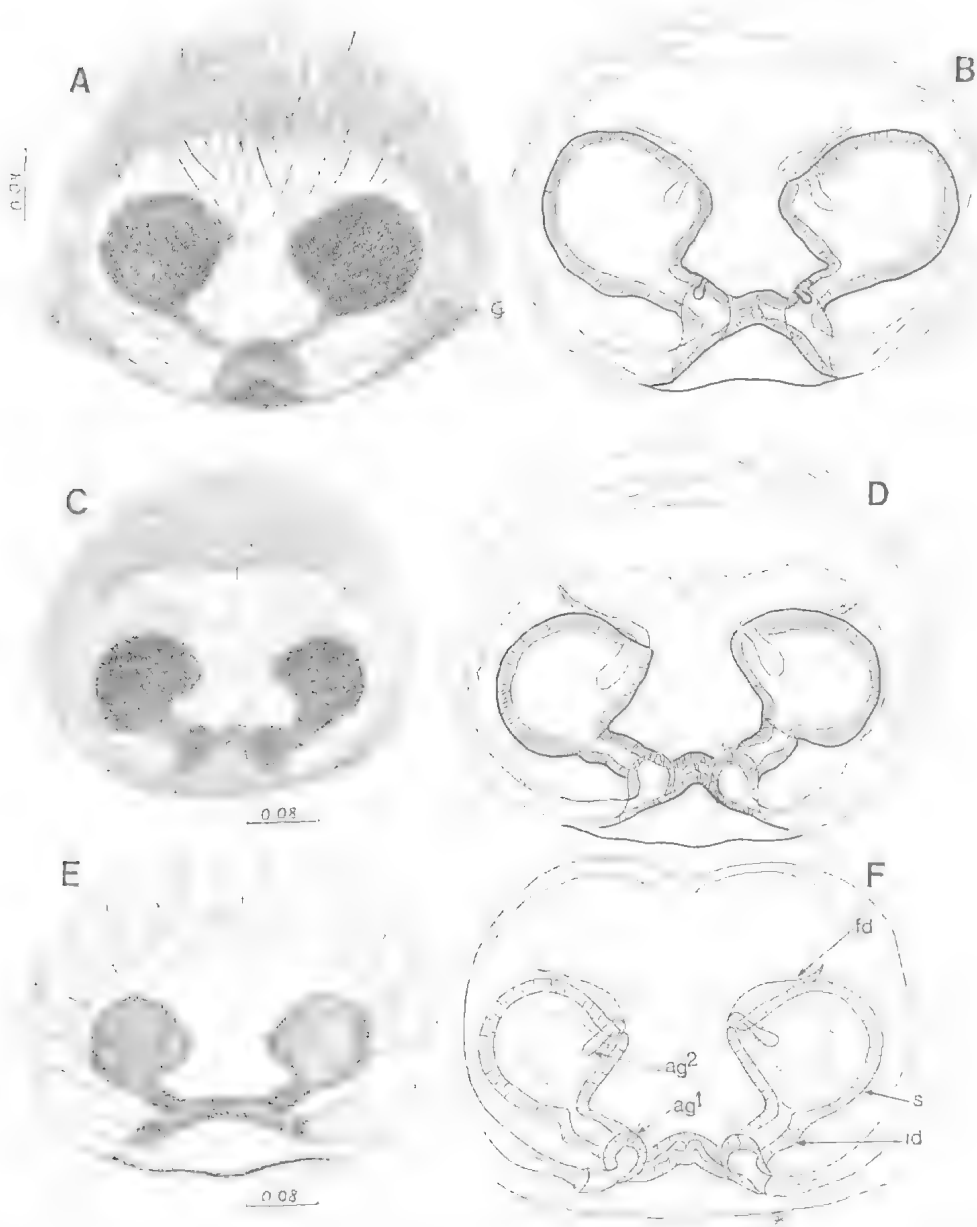


FIG. 3. *Thorelliola ensifera*, epigynes and its internal structures. A-B, from Sulawesi; C-D, from Tahiti; E-F, comparative material from Sulawesi.

dark hairs. Surroundings of eyes black with some dark, long and stiff hairs. Abdomen (Fig. 1A) oval, shiny and yellow, with pattern of black and gray markings and three whitish spots in front of spinnerets. Anterior part of abdomen with scattered protruding, long hairs. Spinnerets light yellow, with fine, dark hairs. Clypeus (Fig. 1B) low, pale brown with two large, distinctive setae

(horns) in the centre. Chelicerae (Fig. 1C), maxillae and labium yellow-beige. Sternum and coxae pale yellow. Legs yellow-grey, covered with numerous dark hairs and some spines. Venter light yellow with some black markings, especially on the lateral parts.

Palpal organ (Fig. 1D-E). Embolus thinner than in other species, seminal duct meandering. Retro-



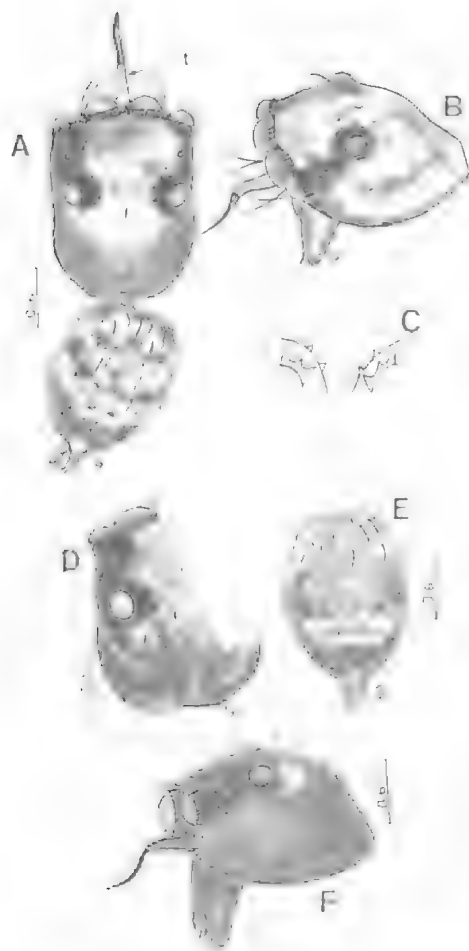


FIG. 4. *Thorelliola biapophysis* sp. nov., ♂♂. A-C, from Ambon; D-F, from Banda Islands. A-B, D-E, general views. C, cheliceral teeth.

lateral tibial apophysis rather slender, not furcated. Prolateral tibial apophysis with robust spine.

Dimensions. CL 2.28, CW 1.80, CH 1.44, AL 2.16, AW 1.80, AEW 1.56, PEW 1.49, EFL 1.02.

Female. Cephalothorax (Fig. 2A-B, C-D) moderately tall, orange-brown, darker posteriorly, covered with fine, whitish hairs. Eyes surroundings black with fringes of fine, white hairs and long, brown bristles, especially above anterior eyes. Abdomen oval, shiny, anteriorly whitish-beige, posteriorly black-grey. Pattern of markings shows some variability (Fig. 2A, D), but three white spots on the posterior dorsal abdomen are always conspicuous. Spinnerets thin, whitish-grey, with paler tips. Clypeus (Fig. 2B, E) low,

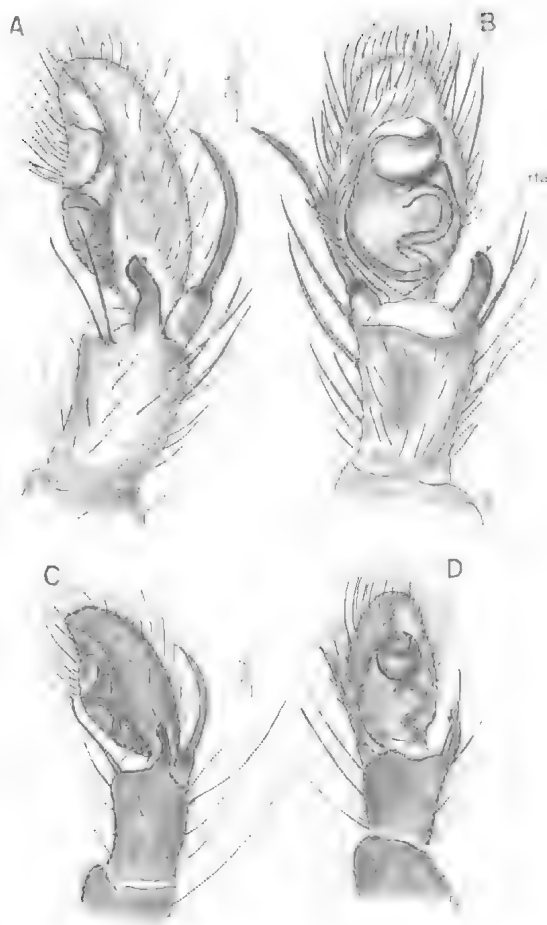


FIG. 5. *Thorelliola biapophysis* sp. nov., palpal organs, lateral and ventral views. A-B, from Ambon; C-D, from Banda Islands.

beige to brown, with two protruding setae — more delicate than in the ♂. Chelicerae (Fig. 2C, F) orange-brown, without lateral cusps. Maxillae and labium orange with paler tips. Sternum yellow, heart-shaped. Legs yellow-orange, darker distally, with some black markings. Venter whitish with a few black or whitish dots. Palps yellow. Epigyne (Fig. 3A-D) transverse oval, in comparison to the other species spermathecae more spherical.

Dimensions. CL 1.92, CW 1.53, CH 1.11, AL 2.16, AW 2.28, AEW 1.56, PEW 1.44, EFL 1.04.

DISTRIBUTION, Malaysia, Indonesia, Polynesia, Melanesia, Hawaii, Tahiti, Singapore.

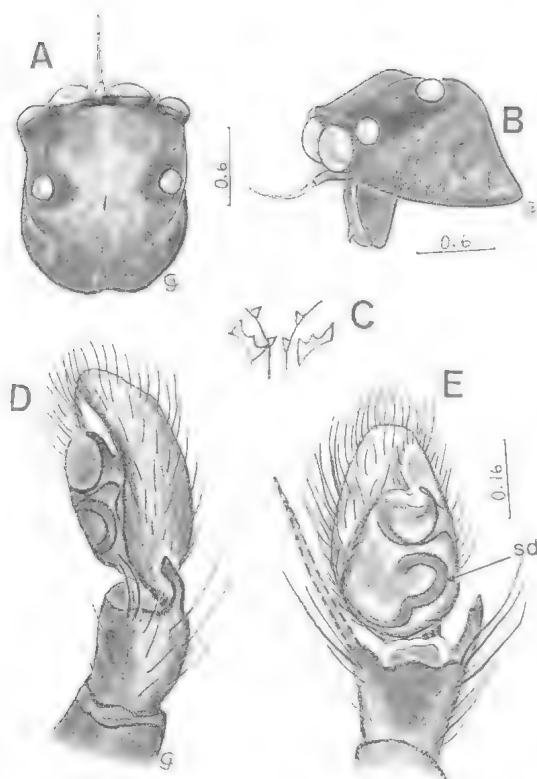


FIG. 6. *Thorelliola glabra* sp. nov., ♂ from Banda Islands. A-B, cephalothorax, dorsal and lateral views (horns on the tip of truncus reconstructed). C, cheliceral teeth. D-E, palpal organ, lateral and ventral views (pta with the reconstructed spine).

***Thorelliola biapophysis*  
sp. nov. (Figs 4-5)**

**MATERIAL EXAMINED.** HOLOTYPE. QMS35299, ♂, Ambon: Hila, forest, from bark with ants, 29-31.01.95, C.L. Deeleman-Reinhold. PARATYPE. QMS35300, ♂, Banda Islands: Lonthoir, Namulu, 21.01.1995, C.L. Deeleman-Reinhold.

**DIAGNOSIS.** ♂♂ with the trunk on the clypeus; in comparison to *T. glabra*, and *T. truncilonga* truncus of the middle length. Posterior part of abdomen dark with one white spot in front of spinnerets.

**DESCRIPTION.** Male. Cephalothorax (Fig. 4A-B, D, F) moderately tall, brown-beige to brown, with scattered brown hairs. Surroundings of eyes black with fine whitish or brown hairs. Abdomen (Fig. 4A, E) nearly oval, covered with reflecting scales, yellow-whitish-black, with pattern of some dark spots and markings. One whitish spot in front of yellow-grey spinnerets. Clypeus low,

brown-grey to brown with trunk ended by two protruding horns. Chelicerae (Fig. 4C), maxillae and labium brown. Sternum heart-shaped, yellow, covered with fine, brown hairs. Legs yellow-brown, tarsi and metatarsi paler. Coxae I and II darker than the others. Venter pale grey.

Palpal organ (Fig. 5A-D). Embolus rather short and robust; retrolateral tibial apophysis wide, apically forked; two protruding setae near the retrolateral tibial apophysis. Prolateral tibial apophysis slightly dislocated dorso-laterally.

Dimensions. CL 1.85, CW 1.35, CH 1.06, AL 1.45, AW 1.20, AEW 1.44, PEW 1.27, EFL 0.98. Female unknown.

**DISTRIBUTION.** Ambon, Banda Islands.

**ETYMOLOGY.** From the structure of retrolateral tibial apophysis, which is divided apically.

***Thorelliola glabra* sp. nov.  
(Fig. 6)**

**MATERIAL EXAMINED.** HOLOTYPE. QMS35301, ♂, Banda Islands, Moluccas, Neira, 02.1995, C.L. Deeleman-Reinhold.

**COMPARISON.** Differs from *T. biapophysis* by the course of seminal duct, trunk shorter.

**DESCRIPTION.** Male. Cephalothorax (Fig. 6A-B) tall, brown; scarce hairs only around the anterior eyes; eyes surroundings black. Abdomen missing. Clypeus low, brown; trunk rather short. Chelicerae (Fig. 6C), maxillae and labium brown.

Palpal organ (Fig. 6D-E). The course of seminal duct similar to the upturned figure 3.

Dimensions. CL 1.80, CW 1.38, CH 1.08, AEW 1.40, PEW 1.25, EFL 0.96.

Female unknown.

**DISTRIBUTION.** Banda Islands.

**ETYMOLOGY.** From the Latin word *glabrus* = smooth.

***Thorelliola javaensis* sp. nov.  
(Figs 7-8)**

**MATERIAL EXAMINED.** HOLOTYPE. QMS35302, ♂, Java: Cibodas National Park, 1450m, from leaves, 10.12.1986, Suharto Djojosedharmo. ALLOTYPE. QMS35303, ♀, same data. PARATYPES. QMS35304, ♂, 7 ♀, same data.

**DIAGNOSIS.** Dark brown stripes on the cephalothorax. Embolus in palpal organ (Fig. 7F-G) longer and thin, seminal duct not meandering; no

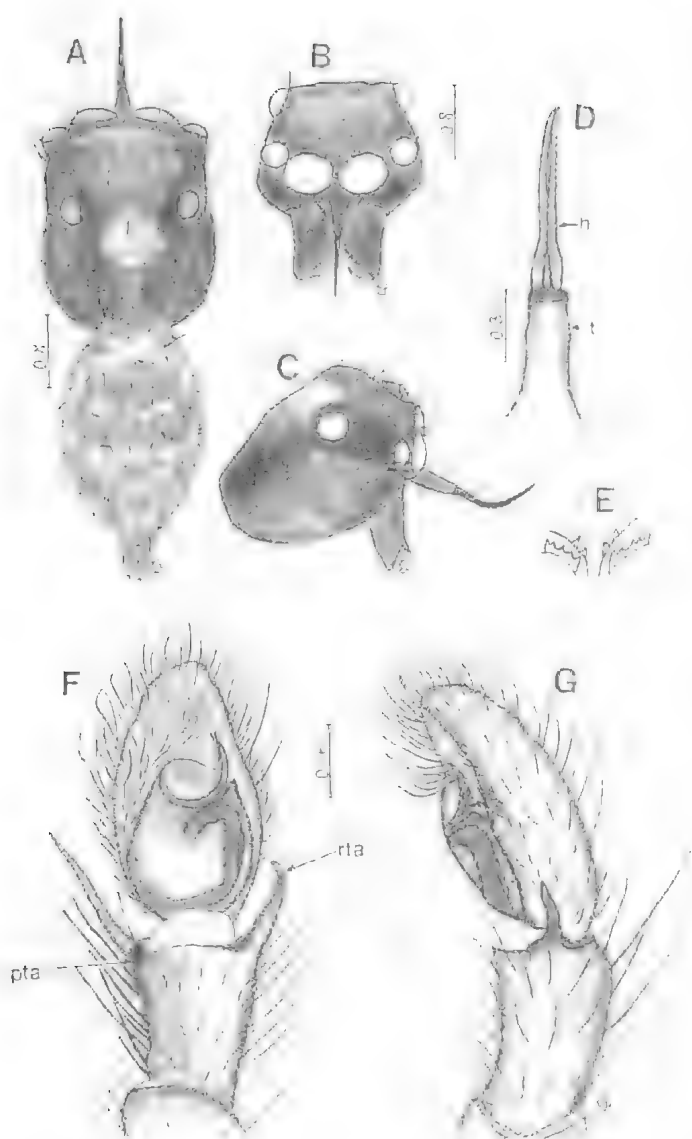


FIG. 7. *Thorelliola javaensis* sp. nov., ♂ from Java. A-C, general views. D, truncus. E, cheliceral teeth. F-G, palpal organ, ventral and lateral views.

bristles near the retrolateral tibial apophysis, the latter is slender and not furced apically. Spermathecae of different shape (Fig. 8E-F).

**DESCRIPTION.** Male. Cephalothorax (Fig. 7A-C) tall, brown-beige in the eye field and yellow around fovea, with two thoracic stripes. Surroundings of eyes black. Abdomen (Fig. 7A) grey-beige with some darker spots and dots. Spin-

nerets dark grey, with lighter tips. Clypeus (Fig. 7B) very low, brown, with the trunk (Fig. 7D) ended by two long horns. Chelicerae (Fig. 7E) brown; maxillae and labium orange with paler tips. Sternum heart-shaped with brown margins and covered with brown, short hairs. Legs I brown, darker and more robust than the others; tarsi yellow. Venter grey, with no spots.

Palpal organ (Fig. 7F-G). Embolus rather thin; seminal duct non-meandering; retro-lateral tibial apophysis rather slender and slightly bended apically; prolateral tibial apophysis short, with the robust spine.

**Dimensions.** CL 2.04, CW 1.68, CH 1.32, AL 2.28, AW 1.44, AEW 1.68, PEW 1.50, EFL 1.08.

**Female.** Cephalothorax (Fig. 8A-C) tall, yellow-beige, with two distinctive, brown stripes, generally paler than that in the ♂. Surroundings of eyes dark brown. Eye field covered with the fine, white hairs. Abdomen near oval, of the similar colour pattern as in ♂, but a little darker. Spinnerets yellow-grey. Clypeus (Fig. 8C) rather low, orange, with two protruding central setae. Chelicerae (Fig. 8D), maxillae and labium orange. Sternum pale yellow, covered with fine, brown, hairs. Legs yellow, with dark grey markings, especially near the joints. Palps yellow-beige. Venter pale grey.

Epigyne (Fig. 8E-F). Spermathecae less spherical than in other species, with different shape of fertilization ducts (Fig. 8F).

**Dimensions.** CL 1.94, CW 1.45, CH 1.14, AL 2.33, AW 1.78, AEW 1.51, PEW 1.36, EFL 0.90.

**DISTRIBUTION.** Java; Cibodas N.P.

**ETYMOLOGY.** From the locality

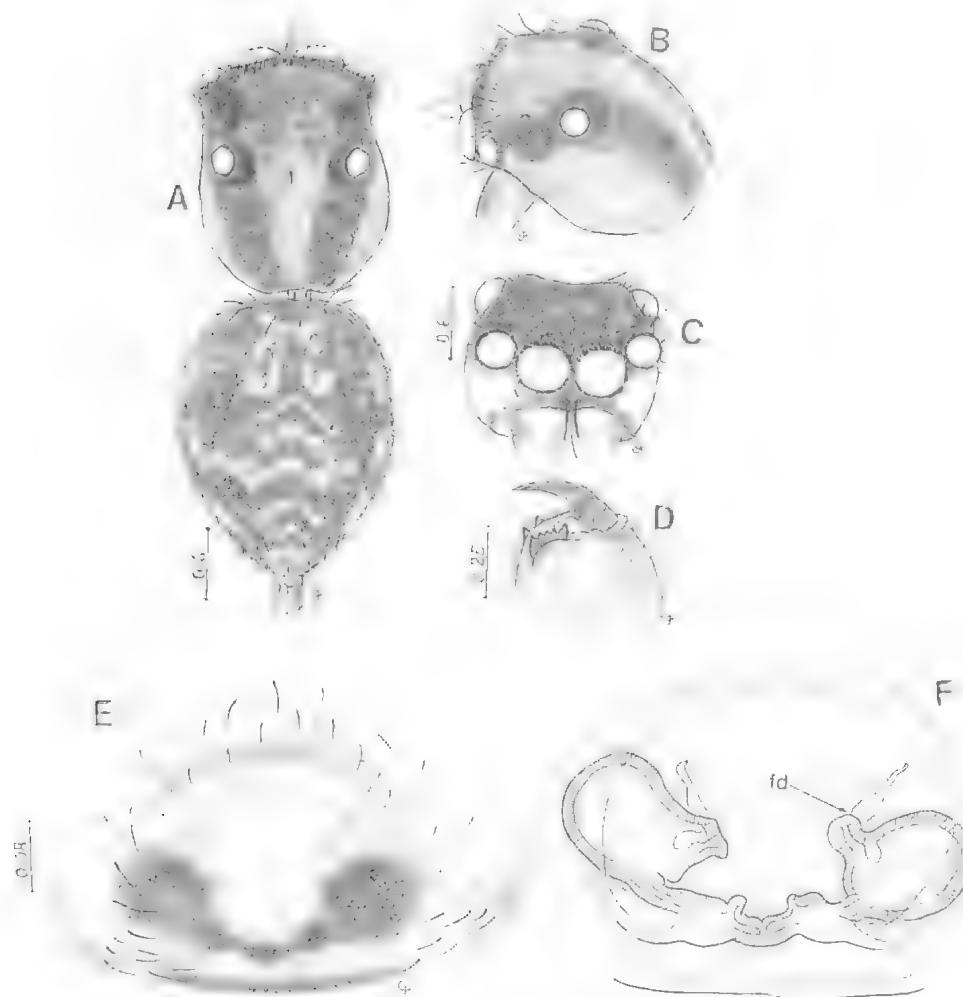


FIG. 8. *Thorelliola javaensis* sp. nov., ♀ from Java. A-C, general views. D, cheliceral teeth. E-F, epigyne and its internal structures.

***Thorelliola truncilonga* sp. nov.**  
(Figs 9-10)

**MATERIAL EXAMINED.** HOLOTYPE. QMS29963, ♂, Papua New Guinea, Central Province, National Capital District, House Pomoms, (possibly escaped from Yule Islands' litter), left palp missing, 20.08.1985, D.J. Court. ALLOTYPE. QMS29964, ♀, Port Moresby, Botanic Garden, on foliage, 28.06.1988, D.J. Court.

**DIAGNOSIS.** Male truncus long and robust, ended by two short setae. Prolateral tibial apophysis short and with no spines. Shape of spermathecae and course of insemination ducts different than in other species.

**DESCRIPTION.** Male. Cephalothorax (Fig. 9A-B) tall, orange-brown, darker posteriorly. Eyes surroundings black, covered with brown hairs. Abdomen oval, orange-black, with a pattern of dark brown and grey spots. One white spot in front of the spinnerets. Spinnerets yellow, with brown markings laterally. Clypeus (Fig. 9B) rather low, brown, with sparse, brown bristles and a massive trunk ended by two protruding, but short horns. Chelicerae (Fig. 9C), maxillae and labium brown with lighter tips. Sternum broad and yellow. Legs brown-orange, covered with brown hairs, more numerous distally. Venter yellow-grey with some small greyish lateral spots.

Palpal organ (Fig. 9D-F). Embolus more robust than in the other species; prolateral tibial apoph-

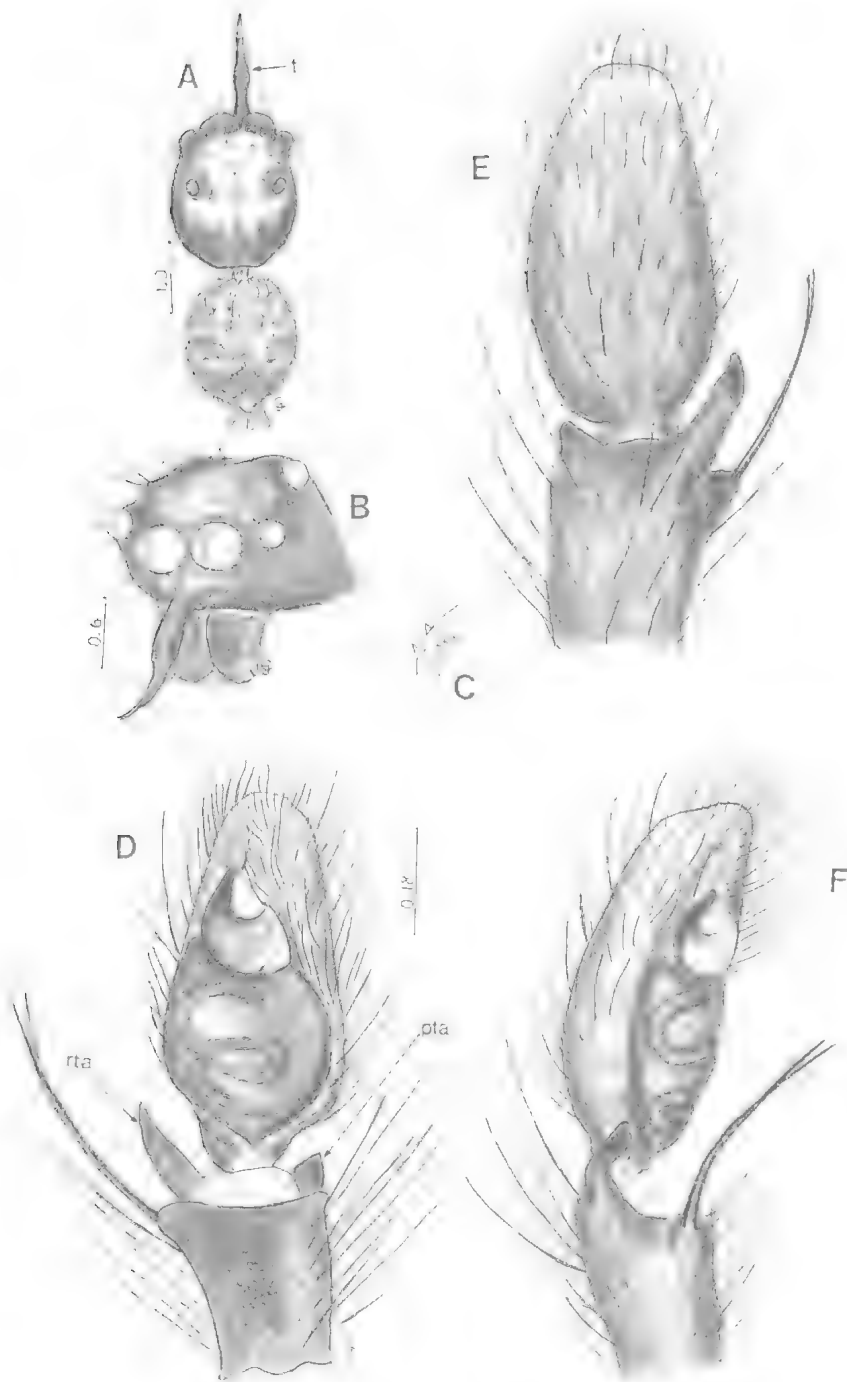


FIG. 9. *Thorelliola truncilonga* sp. nov., ♂ from Papua New Guinea. A-B, general views. C, cheliceral teeth. D-F, palpal organ, ventral, dorsal and lateral views.

ysis short, with no spines; near the retrolateral tibial apophysis — an appendix with two long spines.

Dimensions. CL 2.40, CW 2.10, CH 1.45, AL 2.05, AW 1.70, AEW 1.80, PEW 1.70, EFL 1.02.

Female. Cephalothorax (Fig. 10A-B) tall, yellow-beige with dark brown markings. Surroundings of eyes black, covered with sparse, stiff brown hairs. Abdomen (Fig. 10A) oval, yellow-beige, with the pattern of grey and black triangle-like markings and with scattered brown hairs. Spinnerets yellow-grey. Clypeus pale yellow with sparse amber bristles. Chelicerae (Fig. 10C) yellow orange. Maxillae and labium similar in colour, with darker tips. Sternum pale yellow. Legs yellow with brown markings, especially around joints. Venter pale yellow, with small dark brown spots laterally.

Epigyne (Fig. 10D-E).

Dimensions. CL 1.80, CW 1.40, CH 1.16, AL 1.60, AW 1.45, PEW 1.25, AEW 1.35, EFL 0.90.

**DISTRIBUTION.** Papua New Guinea: Port Moresby.

**ETYMOLOGY.** From the structure of the trunk.

#### ACKNOWLEDGEMENTS

We wish to thank Dr C. Deeleman-Reinhold (Ossendrecht) and Mr D.J. Court (Singapore) for providing specimens to this study. We are also grateful to Dr M. Zabka and Prof. Prószyński for critical review of the typescript.

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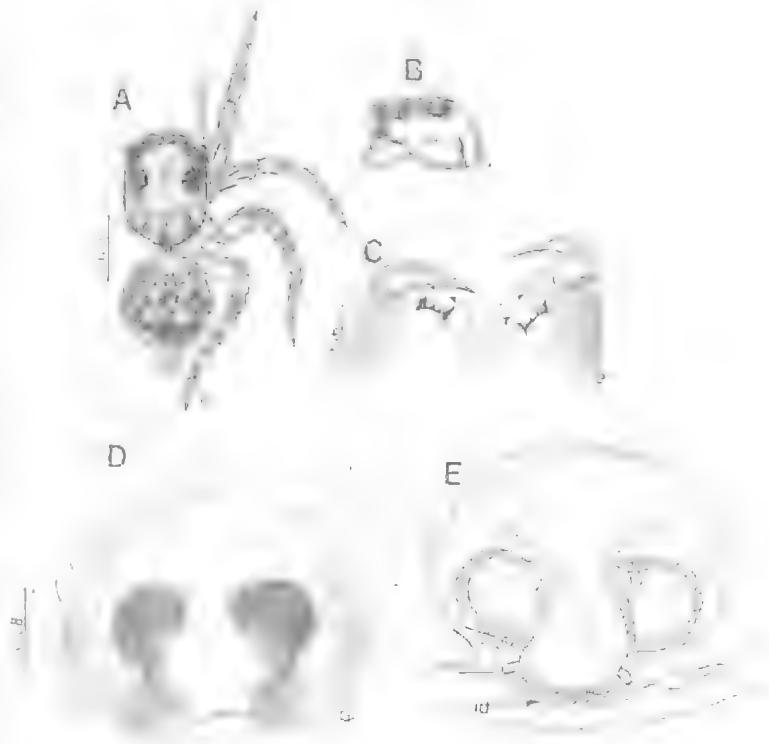


FIG. 10. *Thorelliola truncilonga* sp. nov., ♀ from Papua New Guinea. A-B, general views. C, cheliceral teeth. D-E, epigyne and its internal structures.

## CRETACEOUS FRESHWATER BIVALVES FROM QUEENSLAND

SCOTT A. HOCKNULL

Hocknull, Scott A. 1997 06 30: Cretaceous freshwater bivalves from Queensland. *Memoirs of the Queensland Museum*. **42**(1): 223-226. Brisbane. ISSN 0079-8835.

Three new freshwater unioids are described from the Griman Creek and Winton Formations. *Protovirgus wintonensis* sp. nov. is a medium-sized elongate unioid with the anterior adductor muscles raised on a platform. *Prohyria macmichaeli* sp. nov. is characterised by its more anteriorly placed umbones and its less robust form in comparison to other members of the genus. *Velesunio goondiwindiensis* sp. nov. is small, elongate-ovoid with finer growth lines than most members of the genus. All three taxa range from middle Albian to Cenomanian. □ *Unionida*, *Prohyria*, *Protovirgus*, *Velesunio*, *Winton Fm.*, *Griman Creek Fm.*

Scott A. Hocknull, *Queensland Museum PO Box 3300 South Brisbane, Queensland Australia 4101*; 2 January 1997.

Collections made from the middle Cretaceous Winton and early Cretaceous Griman Creek Formations have yielded three new taxa; *Protovirgus wintonensis* sp. nov., *Prohyria macmichaeli* sp. nov. and *Velesunio goondiwindiensis* sp. nov. The Griman Creek Fm. (Exon & Senior, 1976) is a non-marine to brackish unit which outcrops in the Surat Basin. It is considered to be of middle Albian age by Burger (1986, 1995) who placed the unit within the *Coptospora paradoxa* Zone. The younger Winton Fm. out-crops extensively within the central and southwestern Eromanga Basin being of latest Albian to Cenomanian age and is, except for its extremities, a bare and exclusively freshwater deposit, comprising lacustrine and fluvial siliciclastic sediments. McLoughlin et al. (1995) described the Cenomanian flora from the Winton Fm. Localities are prefixed QML and are detailed in the appendix.

Newton (1915) erected *Unio whitecliffensis* and *Unio jaqueti* respectively from the Coreena Fm. of White Cliffs and the Griman Creek Fm. of Lightning Ridge. McMichael (1956) revised this material and assigned *U. jaqueti* to *Velesunio* and *U. whitecliffensis* to *Hyridella*. The two specimens figured by Dettman et al. (1992) are here assigned to *Velesunio goondiwindiensis* (Dettmann et al., 1992: 244, Fig 19(j)) and *Protovirgus wintonensis* (Dettmann et al., 1992: 244, Fig 19(i)).

List of Cited Localities. QML229: Mculler Range, west of Cork Station, near Winton, CWQ, Winton Formation, Cenomanian. QML379: Franklin Station, 'Trevor Cluff's' locality in paddock west of Mt Gideon below small tabletops and west on flats towards hills, near Winton, CWQ, Winton Formation, Cenomanian. QML570: Te Apiti Stn, NW of Goondiwindi,

SEQ, Dam site. Griman Creek Formation. Late Albian.

### SYSTEMATIC PALAEONTOLOGY

Phylum MOLLUSCA

Class BIVALVIA

Order UNIONOIDA Stoliczka, 1871

Family MUTELIDAE Gray, 1847

**Protovirgus McMichael, 1956**

***Protovirgus wintonensis* sp. nov.**  
(Fig 1. A-E)

Unioid, Dettmann et al. 1992: 244, fig. 19(i).

ETYMOLOGY. For the town of Winton.

MATERIAL EXAMINED. HOLOTYPE: QMF-34635, L379; Franklin Stn. Trevor Cluff's locality, Mt Gideon. PARATYPES: QMF5681-5682, QMF34645, QMF34646 from QML570; QMF34634, QMF34644, QMF34647, QMF34648 from QML379.

DIAGNOSIS. Small to medium-sized, equivalved, elongate unioid with slightly inflated umbones and fine, comarginal ornament. Hinge straight; anterior adductor muscle raised on platform. Tapering fairly strongly with well-rounded posterior margin.

DESCRIPTION. Maximum height ranges from 27-34mm, width 19-30mm and length 70-80mm (Table 1). Shell elongate, hinge straight, ligament thin, extending approximately 2/3 of shell length. Fine comarginal ornament of growth lines. Rounded posterior margin. Beak unsculptured. Shell thin. Anterior adductor muscle positioned behind umbo, raised on platform. Posterior muscle scar unknown. Dentition unknown.

**REMARKS.** The tapering form, sharp ventral margins and strongly anterior umbones are typical of *Protovirgus*. The type species, *P. dunstani* (Elthridge Jr 1888, described by McMichael, 1956: 232, fig. 8) from the Triassic of NSW is approximately half the length and much more linguiform than *P. wintonensis*. *P. flemingi* McMichael (1956: 232-233, fig. 1-3) from the Cretaceous of New Zealand is approximately two-thirds the size, and the umbones are placed more posteriorly than in *P. wintonensis*. *P. jaenschi* Ludbrook, 1961 from the Triassic of SA is slightly larger at 80mm long, 31mm high, and has a less developed muscle scar and is more ovate than *P. wintonensis*. *P. jaenschi* has an inflexion in the posterior 1/3 which is not seen in *P. wintonensis*. *P. coatsi* Ludbrook, 1961 from the Triassic of Leigh's Creek is smaller (two-thirds the length) with more concave ventral and convex dorsal margins. *P. clellandi* Hocknull, 1994 from the Triassic of Ipswich, south-east Queensland is much larger, the holotype being 123mm long and 39mm high, and is sharper posteriorly with greater inflation of the umbones.

#### *Prohyria* McMichael, 1956

##### *Prohyria macmichaeli* sp. nov. (Fig. 1. F-H, Fig. 2. A-C)

**ETYMOLOGY.** For Donald F. McMichael for his studies of freshwater bivalves.

**MATERIAL EXAMINED.** HOLOTYPE: QMF34636, QML379; Franklin Stn. Trevor Cluff's locality, Mt. Gideon. PARATYPES: QMF5677 from QML570 and QMF34637 from QML379, QMF34638 from QML229.

**DIAGNOSIS.** Medium-sized, equivalved unioid, ovate, rugose ornament, umbones anterior and inflated, beak slightly sculptured, shell thick.

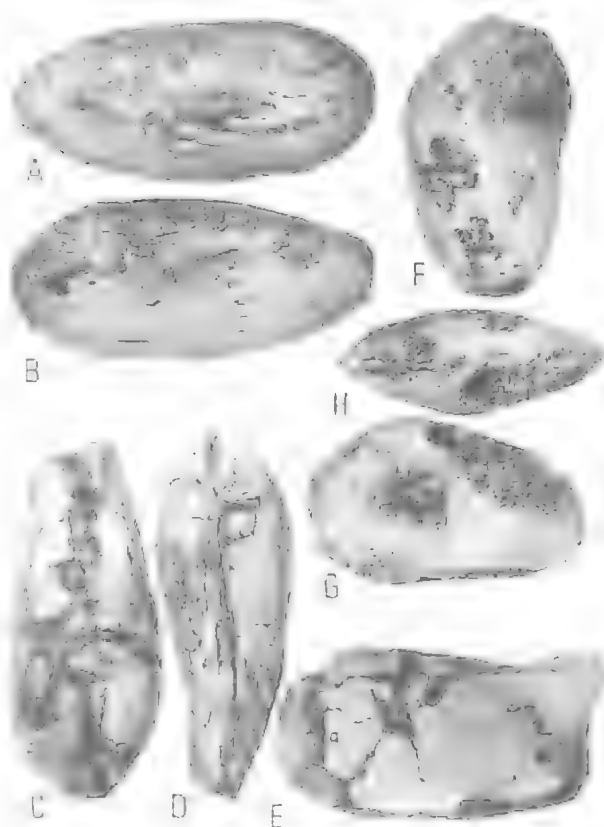


FIG. 1. A-E, *Protovirgus wintonensis* sp. nov. A-C, Holotype QMF34635, x 1.2 (A, right valve; B, left valve; C, dorsal view). D, E, Paratype QMF34634, internal mold x 1.2 (D, dorsal view; E, left valve). F-H, *Prohyria macmichaeli* sp. nov. Paratype QMF34638 x 1.2 (F, right valve; G, left valve; H, dorsal view).

**DESCRIPTION.** Maximum height 32mm, width 27mm and in length 55mm (Table 2). Elongate-ovate, umbones anterior and inflated. Anterior margin convex, ornament rugose, beak slightly

TABLE 1. Morphometric data for specimens of *Protovirgus wintonensis* sp. nov. from the Winton and Griman Creek Formations. Measurements in mm.

Specimen	Height	Length	Width
QMF34635	27	70	25
QMF34636	30	75	25
QMF34644	34	82	30
QMF34645	25	50	20
QMF34646	22	54	19
QMF34647	30	73	27
QMF34648	33	75	25
QMF5682	17	38	14
QMF5681	19	47	16



sculptured. Hinge straight, short. Shell thick, ligament short, and thick. Escutcheon relatively broad, anterior adductor muscle small, raised slightly and orientated anteroventrally. Dentition unknown.

**REMARKS.** The anteriorly placed, inflated umbones, rugose ornament, elongate-ovoid shape ally the present material to *Prohyria*. The type species, *P. johnstoni* (Ethridge Jr, 1881) of McMichael (1956: 227-228, figs 6&7) from the Oligocene of Tasmania is much larger, up to 126mm long, wider (up to 55mm) and the dorsal margin is sharper. *P. eyrensis* (Etheridge, 1892) of McMichael (1956: 228-230, figs 8-12) from the Triassic of Leigh's Creek, South Australia is also longer (up to 102mm), wider (up to 50mm), and umbones are placed more posteriorly than *P. macmichaeli*.

**Velesunio** Iredale, 1934

***Velesunio goondiwindiensis***  
sp. nov.  
(Fig. 2. D-J.)

Unioïd, Dettmann et al. 1992: fig. 19j.

**ETYMOLOGY.** For the town of Goondiwindi.

**MATERIAL EXAMINED.** HOLOTYPE: QMF5684, from QML570; Dam at 'Te Apiti' Stn., near Goondiwindi, SEQ. PARATYPES: QMF5683, QMF5685, QMF5686, QMF34639-34641 from QML570.

**DIAGNOSIS.** Small, elongate-ovoid, fine comarginal ornament and thin shell. Umbones anterior. Anterior adductor muscles small, elongate, raised slightly. Shell expanded posteroventrally.

**DESCRIPTION.** Small, equivalved unioïd. Elongate-ovoid, compressed with fine comarginal ornament. Maximum height ranges 33-35mm, width 16-18mm and length 35-38mm (Table 3). Umbones placed anteriorly, at anterior 1/3 of total length. Beak sculptured but small. Dorsal and

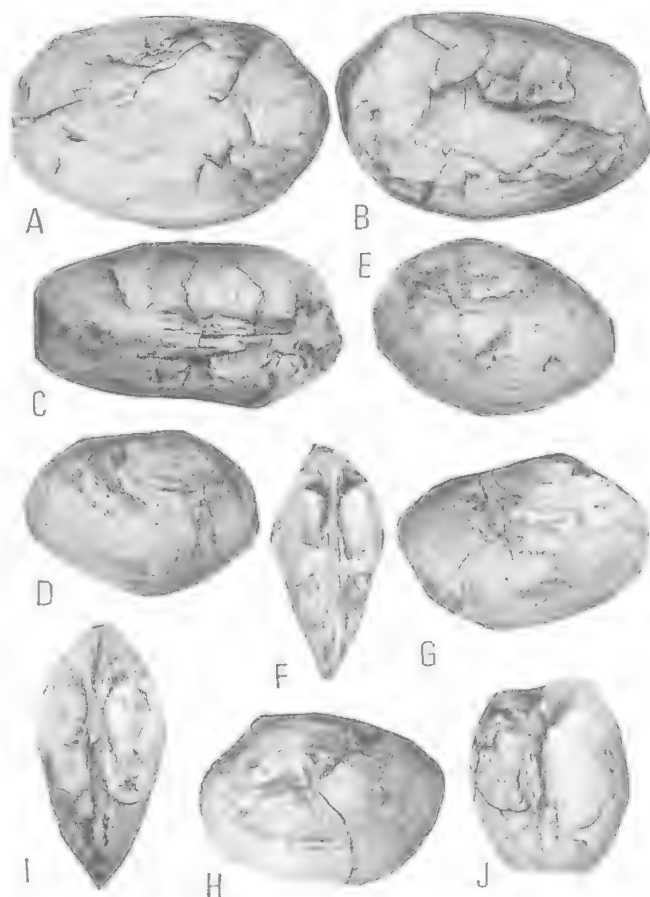


FIG. 2. A-C, *Prohyria macmichaeli* sp. nov. Holotype QMF34637, x 1.2 (A, right valve; B, left valve; C, dorsal view). D-J, *Velesunio goondiwindiensis* sp. nov. D-F, Paratype QMF34639, x 1.2 (D, right valve; E, left valve; F, dorsal view). G-I, Holotype QMF5684, x 1.2 (G, right valve; H, left valve; I, dorsal view). J, Paratype QMF34640, x 1.2, dorsal view.

ventral margins run subparallel, forming an expanded posterior. Hinge 1/2 the length of total. Ligament thin, escutcheon narrow. Maximum height posterior to umbones. Adductor muscle scars small, elongate and orientated anteroventrally. Dentition unknown.

**REMARKS.** The elongate-ovoid, anteriorly placed umbones with subparallel dorsal and ven-

TABLE 2. Morphometric data for the specimens of *Prohyria macmichaeli* sp. nov. from the Winton and Griman Creek Formations.

Specimen	Height	Length	Width
QMF34636	27	48	23
QMF34637	32	55	27
QMF34638	28	50	20

TABLE 3. Morphometric data for the specimens of *Velesunio goondiwindiensis* sp. nov. from the Winton and Griman Creek Formations. Measurements in mm.

Specimen	Height	Length	Width
QMF5683	22	22	15
QMF5684	26	35	18
QMF5685	23	29	13
QMF5686	22	31	15
QMF34639	24	36	15

tral borders expanding posteriorly indicate *Velesunio* Iredale, 1934. *V. jaqueti* (Newton, 1915) of McMichael (1956: 240) from the Griman Creek Formation of Lightning Ridge is larger, more elongate (37-42mm long) and narrow (12-15mm) with umbones placed more posteriorly than *V. goondiwindiensis*. All recent species of *Velesunio* are much larger, more robust and have a more pronounced winged posterior (McMichael & Hiscock, 1958) than *V. goondiwindiensis*.

#### ACKNOWLEDGEMENTS

I would like to thank Alex Cook, Natalie Camilleri and Paul Tierney for their help and encouragement. The described material was collected by Mary Wade, H.J. McMilland and Ralph E. Molnar.

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**PSEUDANTHESSIUS NEWMANAE, NEW SPECIES (COPEPODA:  
POECILOSTOMATOIDA: PSEUDANTHESSIIDAE) FROM MARINE  
TURBELLARIANS IN AUSTRALIA**

ARTHUR G. HUMES

Humes, A.G. 1997 06 30: *Pseudanthessius newmanae*, new species (Copepoda: Poecilostomatoida: Pseudanthessiidae) from marine turbellarians in Australia. *Memoirs of the Queensland Museum* 42(1): 227-231. Brisbane. ISSN 0079-8835.

*Pseudanthessius newmanae*, a new species of poecilostomatoid copepod, is associated in Australia with the marine turbellarians *Tytthosoceros lizardensis* Newman & Cannon (in press) and two undescribed species of *Pseudobiceros*. The female of the new copepod may be distinguished from its 37 congeners by a combination of characters: the length of the body, the length to width ratio of the caudal ramus, and the shape of the genital double-somite. This is the second species of *Pseudanthessius* recorded as associated with Turbellaria. □  
*Pseudanthessius*, Copepoda, Poecilostomatoida, associates, Turbellaria, Australia.

Arthur G. Humes, Boston University Marine Program, Marine Biological Laboratory, Woods Hole, Massachusetts 02543, U.S.A.; 21 March 1997.

Most of the 37 species in the genus *Pseudanthessius* are associated with marine invertebrates (polychaetes, bivalves, asteroids, echinoids, ophiuroids, crinoids, and holothurians). *Pseudanthessius nemertophilus* Gallien, 1936, lives with a nemertean, *Lineus longissimus* Sowerby, on the Atlantic coast of France. Only one species, *Pseudanthessius latus* Illg, 1949, is associated with Turbellaria (with *Cryptophallus magnus* Freeman, now known as *Kaburakia excelsa* Bock, in Washington and California).

This paper contains the description of a second species of *Pseudanthessius* living with marine turbellarians, this time in Australia.

#### MATERIALS AND METHODS

The copepods, collected by Dr Leslie J. Newman, were preserved in 70% ethanol. They were measured and studied in lactic acid, according to the method described by Humes & Gooding (1964). All figures were drawn with the aid of a camera lucida. The letter after the explanation of each figure refers to the scale at which the figure was drawn.

Order Poecilostomatoida Thorell, 1859  
Family Pseudanthessiidae  
Humes & Stock, 1972  
Genus *Pseudanthessius* Claus, 1889

*Pseudanthessius newmanae*, sp. nov.  
(Figs 1a-g, 2a-k, 3a-j)

MATERIAL EXAMINED. HOLOTYPE. QMW21831, ovigerous ♀, from the polyclad turbellarian

*Pseudobiceros*, undescribed species, under rubble, in a depth of approximately 5m, between South Island and Palfrey Island, Lizard Island lagoon, Queensland, Australia, 14°40'S, 145°28'E, L. Newman and A. Flowers collectors, 5 April 1995. ALLOTYPE: ♂ (QMW21830), from *Pseudobiceros*, undescribed species, sublittoral, under rubble, South Passage, Coral Bay, Eel Bommie, Western Australia Australia, L. Newman and A. Flowers collectors, 5 May 1996. PARATYPES. nonovigerous ♀, QMW21349, same data as for holotype. 2 ♀♀, (1 in QM W21348, other dissected, in the collection of the author), from *Tytthosoceros lizardensis* Newman & Cannon, in press, low water mark, South Island, Lizard Island lagoon, Queensland, Australia, 14°40'S, 145°28'E, L. Newman and A. Flowers collectors, 31 March 1995. 1 ♀, QMW21398, from *Tytthosoceros lizardensis*, under rubble, sublittoral, in a depth of 6m, South Passage, Coral Bay, 'Eel Gardens', Western Australia, Australia, L. Newman and A. Flowers collectors. 4 May 1996. 2 ♀♀, QMW21399, 1 ♂ (QMW21399), from *Pseudobiceros*, undescribed species, sublittoral, under rubble, South Passage, Coral Bay, Eel Bommie, Western Australia Australia, L. Newman and A. Flowers collectors, 5 May 1996.

DESCRIPTION. Female (description based on specimens from *Tytthosoceros lizardensis* at Lizard Island): Body (Fig. 1a) elongate. Average length (not including setae on caudal rami) 1.44mm (1.34-1.54mm) and greatest width 0.66mm (0.60-0.72mm), based on 4 specimens. Greatest dorsoventral thickness 0.35mm. Somite bearing leg I separated from cephalosome by dorsal transverse furrow. Epimera of metasomal somites posteriorly rounded. Ratio of length to width of prosome 1.58:1. Ratio of length of prosome to that of urosome 1.46:1.

Somite bearing leg 5 (Fig. 1b-d)  $70 \times 172\mu\text{m}$ . Genital double-somite in dorsal view  $190 \times 172\mu\text{m}$ , ratio 1.05:1, somewhat swollen laterally in anterior two-thirds, but with sides subparallel in posterior third (width  $115\mu\text{m}$ ). Genital areas located dorsolaterally near middle of double-somite, each area bearing 2 very unequal setae  $31\mu\text{m}$  and  $14\mu\text{m}$  and minute process (Fig. 1d). Three postgenital somites from anterior to posterior  $88 \times 102$ ,  $73 \times 94$ , and  $81 \times 82\mu\text{m}$ .

Caudal ramus (Fig. 1e)  $112 \times 39\mu\text{m}$ , ratio 2.87:1. Outer lateral seta  $62\mu\text{m}$ , dorsal seta  $27\mu\text{m}$ , both smooth. Outermost terminal seta  $96\mu\text{m}$ , innermost terminal seta  $140\mu\text{m}$ , and 2 median terminal setae  $308\mu\text{m}$  (outer) and  $462\mu\text{m}$  (inner), all with lateral setules.

Body surface smooth, but few minute refractile points on caudal ramus (Fig. 1e).

Egg sac (Fig. 1f) elongate, multiseriate,  $995 \times 297\mu\text{m}$ , ratio 3.35:1. Eggs  $68\mu\text{m}$  in average diameter (range  $62\text{--}70\mu\text{m}$ ).

Rostral area subquadrate (Fig. 1g). Antennule (Fig. 2a)  $320\mu\text{m}$  long. Lengths of its 7 segments (measured along their posterior nonsetiferous margins): 16 ( $47\mu\text{m}$  along anterior margin), 101, 26, 52, 49, 31, and  $18\mu\text{m}$ , respectively. Formula for armature: 4, 13, 6, 3, 4 + 1 aesthetasc, 2 + 1 aesthetasc, and 7 + 1 aesthetasc. Several setae unusually long, all smooth. Antenna (Fig. 2b) 4-segmented, with armature 1, 1, 3, and II + 4. Third segment  $27\mu\text{m}$  along outer side,  $22\mu\text{m}$  along inner side; fourth segment  $35\mu\text{m}$  along outer side and  $43\mu\text{m}$  along inner side. Two claws slender,  $40\mu\text{m}$  and  $53\mu\text{m}$ . All elements smooth.

Labrum (Fig. 2c) with 2 elongate linguiform lobes. Mandible (Fig. 2d) with constricted proximal area followed on concave side by transverse row of long spinules, and on convex side by 2 small spiniform processes and minute spinules.

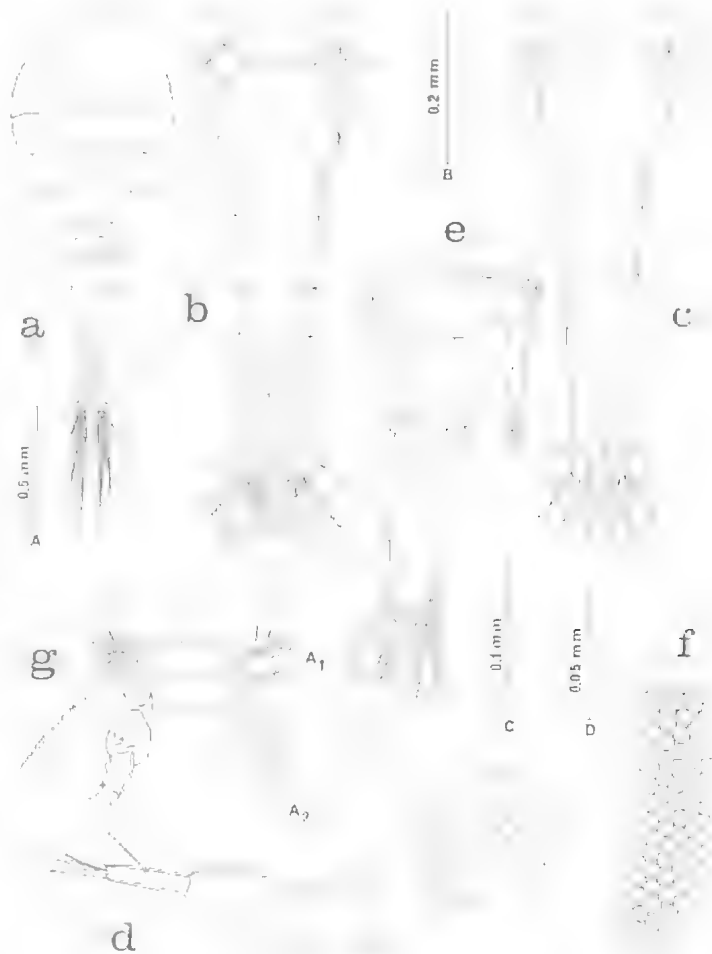


FIG. 1. *Pseudanthessius newmanae*, new species. Female. a, body, dorsal (scale A); b, urosome, dorsal (B); c, urosome, ventral (B); d, urosome, lateral (B); e, anal somite and caudal ramus, dorsal (C); f, egg sac, ventral (D); g, rostral area, ventral (B). A1 = antennule, A2 = antenna.

Lash tapered with very small lateral spinules. Paragnath small lobe. Maxillule (Fig. 2e) with 4 setae. Maxilla (Fig. 2f) with unarmed proximal segment; distal segment with outer small smooth seta and long inner seta bearing unilateral setules. Lash long with outer row of graduated spines. Maxilliped (Fig. 2g) 3-segmented. First segment unarmed, swollen second segment with 2 setae, and small third segment with 2 minute setae and terminating in pointed tip.

Ventral area between maxillipeds and first pair of legs (Fig. 2h) slightly protuberant.

Legs 1-4 (Figs 2i-k, 3a) with 3-segmented rami except 1-segmented endopod in leg 4. Table 1 shows the formula for armature (Roman numerals indicating spines, Arabic numerals representing setae).

Third segment of endopod of leg 1 with outermost seta rather spinelike (Fig. 2i). Leg 4 (Fig. 3a) with exopod 180  $\mu$ m. Endopod 114 x 36  $\mu$ m, ratio 3.17:1, its 2 terminal fringed spines 75  $\mu$ m (outer) and 101  $\mu$ m (inner). Anterior surface of endopod with slight incomplete suggestion of division. Both sides of endopod with long lateral hairlike setules.

Leg 5 (Fig. 1d) without free segment, consisting of slight ridge bearing 2 setae 52  $\mu$ m and 49  $\mu$ m, and adjacent seta 50  $\mu$ m. All setae smooth.

Leg 6 represented by 2 setae, 31  $\mu$ m and 14  $\mu$ m, on genital area (Fig. 1d).

Color of living specimens unknown.

Male (description based on specimens from *Pseudobiceros*, undescribed species, in Western Australia): Body (Fig. 3b) with prosome more slender than in female. Length 1.12mm (1.07-1.19 mm) and greatest width 0.32mm (0.29-0.36mm), based on 3 specimens. Greatest dorsoventral thickness 0.25mm. Ratio of length to width of prosome 1.79:1. Ratio of length of prosome to that of urosome 1.31:1.

Somite bearing leg 5 (Fig. 3c) 36 x 86  $\mu$ m. Genital somite elongate, 130 x 102  $\mu$ m, longer than wide; in lateral view (Fig. 3d) 133 x 101  $\mu$ m. Four postgenital somites from anterior to posterior 57 x 63, 60 x 57, 52 x 52, and 52 x 52  $\mu$ m.

Caudal ramus (Fig. 3c) resembling that of female but smaller, 73 x 25  $\mu$ m, ratio 2.92:1.

Rostrum, antennule, antenna, labrum, mandible, maxillule, and maxilla similar to those in female. Maxilliped (Fig. 3e) with second segment bearing 2 setae and 2 rows of spinules. Claw (Fig.

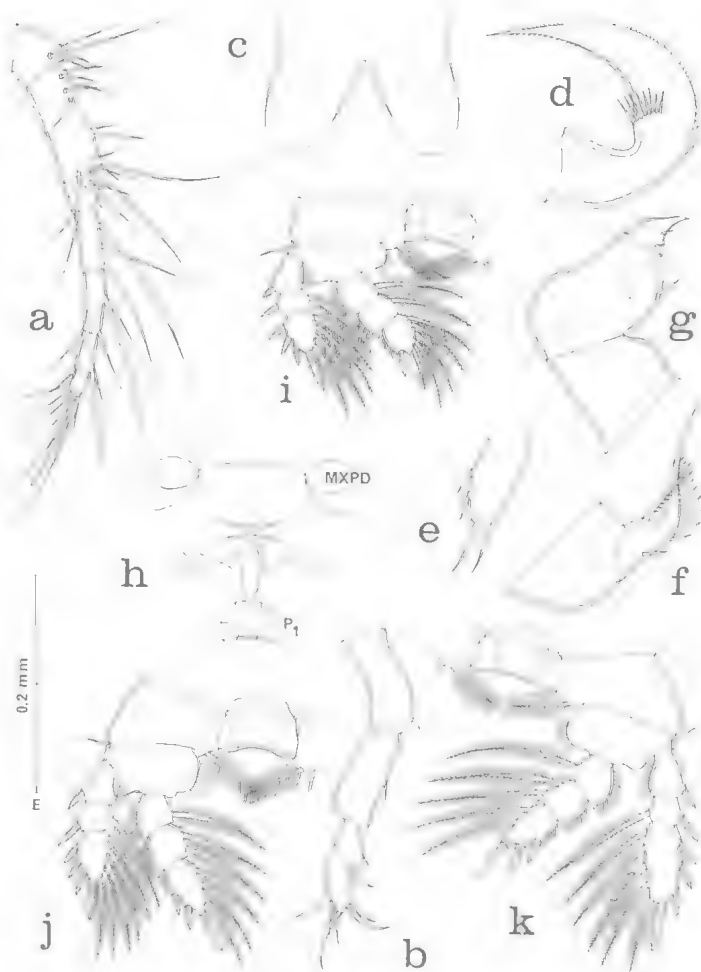


FIG. 2. *Pseudanthessius newmaniae*, new species. Female. a, antennule, dorsal (scale B); b, antenna, posterior (E); c, labrum, ventral (C); d, mandible, dorsal (C); e, maxillule, posterior (C); f, maxilla, inner (C); g, maxilliped, postero-inner (C); h, area between maxillipeds and first pair of legs, ventral (B); i, leg 1 and intercoxal plate, anterior (B); j, leg 2 and intercoxal plate, anterior (B); k, leg 3 and intercoxal plate, anterior (B). MXPD = maxilliped. P1 = leg 1.

TABLE 1. *Pseudanthessius newmaniae*, new species. Formula for armature.

	coxa	basis	exopod		endopod	
P <sub>1</sub>	0-1	1-0	I-0,	I-1; III,I,4	I-0,	0-1; III,I,4
P <sub>2</sub>	0-1	1-0	I-0;	I-1; III,I,5	0-1;	0-2; II,I,3
P <sub>3</sub>	0-1	1-0	I-0;	I-1; III,I,5	0-1;	0-2; II,I,2
P <sub>4</sub>	0-1	1-0	I-0;	I-1; II,I,5	II	

3f) 165  $\mu\text{m}$  long, bearing proximally 2 unequal setae, longer seta with few setules on inner side, and having large terminal lamella and small subterminal tooth.

Ventral area between maxillipeds and first pair of legs as in female.

Legs 1-4 segmented and armed as in female, except for sexual dimorphism in endopod of leg 1, with clawlike process between spine and reduced first seta (Fig. 3g, h).

Leg 5 (Fig. 3d) as in female.

Leg 6 (Fig. 3d, i) postero-ventral flap on genital somite bearing 2 setae.

Spermatophore (Fig. 3j), seen only inside genital somite of male, elongate, 135 x 44  $\mu\text{m}$ .

**ETYMOLOGY.** The new species is named for Leslie J. Newman, University of Queensland, who sent the copepods to me for study.

**REMARKS.** Only one species of *Pseudanthessius* has been recorded as associated with marine flatworms. *Pseudanthessius latus* Illg, 1950, lives on a polyclad turbellarian, *Kaburakia excelsa* Bock (see Faubel, 1983) (= *Cryptophallus magnus* Freeman), on the coasts of Washington and California (Illg, 1950). As Illg (1950) pointed out, Wilson's (1935) specimens of *Pseudanthessius obscurus* (A. Scott, 1909), from large gray flatworms in California, are *P. latus*.

*Pseudanthessius newmaniae* differs from *P. latus* as follows: the average length of the female is 1.44 mm (versus 1.82 mm in *P. latus*), the second segment of the antennule is relatively short (versus exceeding the combined lengths of the five terminal segments in *P. latus*), the ratio of the length to the width of the caudal ramus is 2.87:1 (versus approximately 6:1 in Illg's fig. 1k), and the endopod of leg 4 is elongate (versus inflated in Illg's fig. 1i).

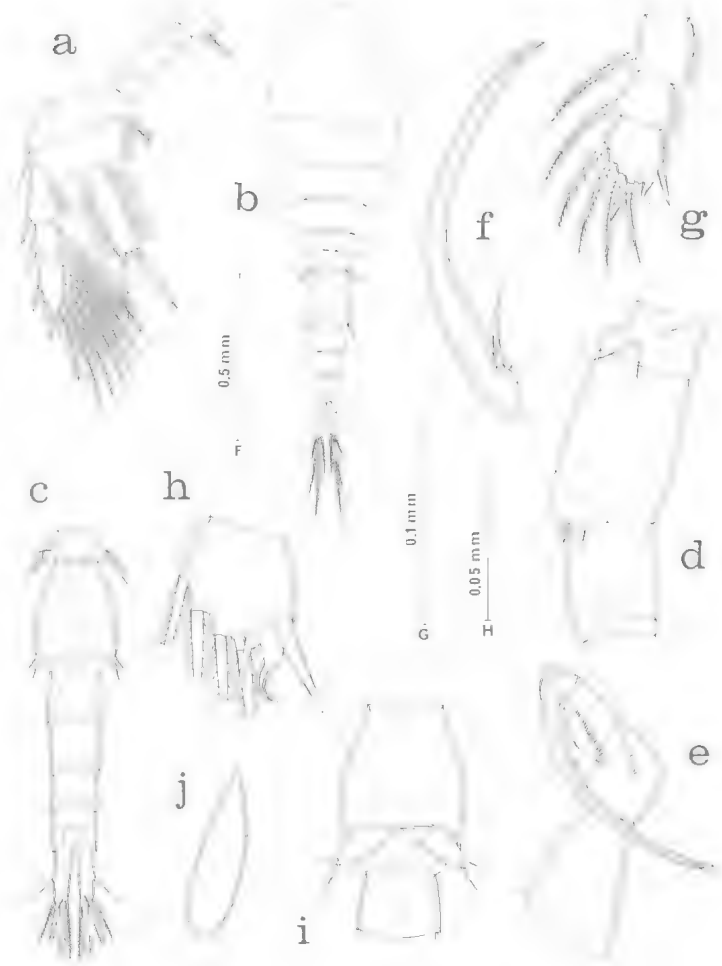


FIG. 3. *Pseudanthessius newmaniae*, new species. Female. a, leg 4 and intercoxal plate, anterior (scale B). Male. b, body, dorsal (F); c, urosome, dorsal (B); d, somite bearing leg 5, genital somite, and first postgenital somite, lateral (E); e, maxilliped, postero-inner (C); f, claw of maxilliped, antero-outer (G); g, endopod of leg 1, anterior (C); h, third segment of endopod of leg 1, anterior (H); i, genital somite and first postgenital somite, showing leg 6, ventral (E); j, spermatophore, inside body of male, lateral (E).

A combination of characters of the female will serve to separate the new species from its 37 congeners. In 16 species of *Pseudanthessius* the length of the body is less than 1 mm. In 12 species the ratio of length to width of the caudal ramus is 3.5:1 or more. In 5 species the ratio of the caudal ramus is less than 2:1. Three species cannot be distinguished from the new species by these criteria, but show other characters by which they may be separated from *P. newmaniae*. In

*Pseudanthessius sauvagei* Canu, 1891, the genital double-somite of the female is slender, about 1.7:1, not laterally expanded, and the fourth segment of the antennule is elongate. In *P. spinifer* Lindberg, 1946, the genital double-somite of the female in dorsal view has pointed lateral processes and the mandible has a long slender blade. In *P. vinulus* Humes, 1977, the genital double-somite of the female is quadrate and the longest seta of leg 5 is longer than the genital somite. In one species, *Pseudanthessius faouzi* Steuer, 1940: 21, the female is unknown. The male of *P. faouzi* differs from the male of the new species in that the length of the body is 0.574 mm, and the caudal ramus is approximately 2:1.

The nature of the sexual dimorphism in the third segment of the endopod of leg 1 of the male, with a clawlike process between the spine and the reduced first seta, is unique among the 22 species of *Pseudanthessius* where males are known and where the endopod of leg 1 has been described or illustrated.

*Pseudanthessius newmaniae* occurs on three species of pseudocerotid worms (two of them undescribed) on both eastern and western coasts of Australia. The nature of the association of the copepods with the flatworms is not known. The copepods move actively on the host, and may perhaps feed on the mucus of the worms. It is of interest that *Typhosoceros lizardensis* is very toxic (L.J. Newman, in correspondence).

#### ACKNOWLEDGEMENTS

I thank Leslie J. Newman for her special effort in collecting the copepods and allowing me to study them.

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**NEW INFORMATION ON PSEUDECHIS PAPUANUS (THE PAPUAN BLACK SNAKE), A MEDICALLY SIGNIFICANT ADDITION TO AUSTRALIA'S REPTILES.** *Memoirs of the Queensland Museum* 42(1): 232. 1997. - *Pseudechis papuanus* Peters & Doria, 1879 (the Papuan Black Snake) is known from "... along the south coast of New Guinea, from Prince Frederik Hendrik Island in Irian Jaya, the Western Province (TransFly and Lake Murray), and the coast of the Central Province and Yule Island" (Parker, 1982). It is rare in Papua New Guinea (Whitaker et al., 1982; O'Shea, 1996), and it has been suggested by Parker (1982), Whitaker et al. (1982) and O'Shea (1996) that its apparent rarity may be attributed to attempted predation on *Bufo marinus* (the introduced Cane or Marine Toad), although these reports are not based on field studies of *P. papuanus*. Published data on its feeding habits differ slightly. Whitaker et al. (1982) regard *P. papuanus* as a frog eater, while O'Shea (1996) states it feeds 'primarily on frogs, but also small mammals, lizards and possibly ground nesting birds'.

*P. papuanus* has a potent venom and is a potentially dangerous snake to humans (Campbell, 1967a, 1967b; Parker, 1982; Whitaker, et al., 1982; and O'Shea, 1996). Campbell & Chesterman (1972) examined the action of its venom and showed it to be 'anticoagulant, fibrinogenolytic and caseinolytic'. Parker (1982) reported that *P. papuanus* caused many fatalities in southern coastal Papua New Guinea and O'Shea (1996) regards it as 'the second most venomous land snake in PNG after the laipani'.

In October 1996, E. Vanderduys, A. McManus and I were conducting a reptile survey of the Torres Strait islands. Mr Manual Namo, Acting Principal of the Saibai Island State School, gave me a snake which had been killed in the local school grounds. It had been held for some time in preservative and no date of collection was recorded.

The snake has been photographed (Fig 1.) and added to the Queensland Museum reference collection (QMJ62555). In the following standard identification characteristics, QMJ62555 from Saibai Island (9°23'S, 142°40'E) is readily referred to *P. papuanus* as defined by Golay (1985) and O'Shea (1996): Midbody scales 19; Ventral scales 221; Subcaudal scales 51, anterior 26 entire. The specimen (in spirit) is immaculate black above and dark grey below, with a pink ventral flush on the chin, posterior body and tail. It is a female with a total length of 158 cm and a tail length of 21 cm. The gut contained 3 spirurid nematodes (*Physaloptera* sp.) but no prey items.

Saibai Is. is only 4 km south of the Papua New Guinea coast. It is thus geographically New Guinean but, politically Australian. It is low-lying and mangrove-fringed with pockets of monsoon forest. Its most conspicuous topographic feature is an extensive mosaic of freshwater and saline swamps. Parker (1982) and O'Shea (1996) note that *P. papuanus* has a preference for swampy areas and its occurrence on Saibai Is. is consistent with their observations. A large freshwater swamp lies only about 100 metres from the school and during the 'wet season' it undoubtedly expands to be very close to the school grounds.

The people of Saibai Is. are familiar with *P. papuanus*, know it as the 'Papuan Black Snake' and regard it as dangerous and abundant. There are no records of *B. marinus* on the island and, given the apparent decline of *P. papuanus* in Papua New Guinea, Saibai Is. may prove to be a stronghold for this species.

The discovery of *P. papuanus* on Saibai Is. adds to the Australian fauna another species of elapid snake known to have inflicted fatal bites or believed capable of doing so. Its congener, *P. australis*, occurs in Papua New Guinea and on Cape York Peninsula, and has recently been recorded on



FIG. 1. *Pseudechis papuanus* (QMJ 62555) from Saibai Is.

Prince Of Wales Island (QMJ62560) between them. To treat bites from both species, Black Snake Antivenom is available. It should be stocked at least in the Thursday Island Hospital and, probably, in the clinic on Saibai Is.

#### Acknowledgements

I thank Mr Manual Namo, Acting Principal of Saibai Island State School, for donating the specimen; Mr Eric Vanderduys and Ms Joan Whittier for the opportunity to participate in their Torres Strait field survey; Department of Agriculture, Hawaii, for funding the field work; Ms Anne McManus for assistance in the field; Mr Jeff Wright (Queensland Museum) for photographing the specimen; Ms Tracy Brown for developing the photograph; Dr Lester Cannon (Queensland Museum) for identifying the nematodes; and Ms Jeannette Covacevich (Queensland Museum) for assisting me in compiling this note.

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SOME NEW AND PREVIOUSLY KNOWN EARTHWORM SPECIES FROM CAPE YORK PENINSULA (ANNELIDA: OLIGOCHAETA: MEGASCOLECIDAE)

B.G.M. JAMIESON

Jamieson, B.G.M. 1997 06 30: Some new and previously known species of earthworms from Cape York Peninsula (Annelida: Oligochaeta: Megascolecidae). *Memoirs of the Queensland Museum* 42(1): 233-270. Brisbane. ISSN 0079-8835.

Ten new species, in five genera, are described from the Cape York Peninsula, Queensland: *Diplotrema attenuata* sp. nov.; *D. scheltingai* sp. nov.; *Neodiplotrema mcdonaldi* sp. nov.; and *Terrisswalkerius mcilwraithi* sp. nov., from the McIlwraith Range; *Diplotrema acropetra* sp. nov., *Neodiplotrema altanmoui* sp. nov., *N. paripunctata* sp. nov., and *Kayarmacia adelphicus* gen. et sp. nov. from Cape Melville National Park; *Terrisswalkerius curbinensis* sp. nov. from Mt Carbine Tableland, and *T. miserlae* sp. nov., from Mt Misery. *Kayarmacia* (= *Rhododrilus*) *queenslandicus* Michaelsen, 1916, is redescribed from the Alice-Mitchell R. National Park, near the type-locality; it is clearly the sister-taxon of *K. adelphicus*. The phylogenetic and biogeographic affinities of these species are briefly discussed. □ *Megascolecidae*, *phylogeny*, *biogeography*, *Oligochaeta*, *Cape York Peninsula*.

B.G.M. Jamieson, Zoology Department, University of Queensland, Brisbane 4072, Australia; 21 March 1997.

The oligochaete fauna of the Cape Melville National Park and of the McIlwraith Range, in North Queensland, has not previously been described. As a result of the assiduous collecting of Mr K.R. McDonald, new megascolecid species from these areas, from Mt Carbine Tableland and from Mt Misery, in the wet tropics, are described. A new genus *Kayarmacia* is erected for one of the new species from Cape Melville and for *Rhododrilus queenslandicus* Michaelsen, 1916, from the Alice-Mitchell River National Park which is redescribed from new material.

Subfamily Acanthodrilinae

Genus *Diplotrema* Spencer, 1900. Emend.  
Jamieson & Dyne, 1976

*Diplotrema acropetra* sp. nov. (Figs 1-4; 39)

TYPE LOCALITY. 14°43'54"S 144°46'45"E, Rocky Peak, Cape Melville National Park, altitude 450m, on sandstone plateau, base of trees where pigs had been digging, edge of *Banksia robur* swamp, K.R. McDonald, P.J. Lethbridge, 4 Apr 1995.

MATERIAL EXAMINED. HOLOTYPE. QMG212027 (includes microscope slide of right genital seta of IX). PARATYPES. P1-9 QMG212028-212036. OTHER MATERIAL. Several not designated types, QMG213391.

DESCRIPTION. Length 38-55mm (H, P1-9), 43mm (H). Width (midclitellar) 1.7-2.4mm (H, P1-9), 2.3mm (H). Segments (longest and short-

est specimen P3 and 9) 163-169, H 166. Pigmentless buff in ethanol. Prostomium large, epilobous 1/2, closed, the lateral margins of the dorsal tongue strongly convergent and concave (H, P1, P3-5) but in P2 protobous with longitudinal grooves on the peristomium giving an impression of an epilobous condition. Peristomium longer than segment II; neither it nor the prostomium bisected ventrally. Dorsal pores poorly visible, commencing on or behind the clitellum (H, P1-5). Setae 8 per segment, commencing on II; in XII, *aa*: *ab*: *bc*: *cd*: *dd* = 7.2: 1.0: 6.6: 0.7: 29.2; or 13.6: 1.9: 12.5: 1.3: 55.1% (H); ventral setal couples of XVIII absent; those of XVII and XIX modified as enlarged penial setae; ventral setae of X forming genital setae. Nephropores not visible. Clitellum (poorly developed in the holotype); in XIII-XVII, annular, but interrupted ventrally in XVII by the prostatic porophores (P1). Male pores not visible. Prostatic porophores 2 pairs, in XVII and XIX, each an elliptical papilla centred approximately in *ab* lines; penial setae protuberant from one or both pairs (H, P1-5); seminal grooves not apparent (H) or a faint outwardly curved (parenthetic) groove connecting the prostate pores on each side (e.g., P4). Genital tumescences: unilateral in X, (H, P1), left (P1, 2); also paired in XI (P2); or absent in X and left only in XI (P3). Genital markings: an unpaired midventral elliptical to rounded oblong pad between the ventral setal couples (in *aa*) in each of intersegmental furrows 13/14-15/16, 16/17, 17/18, 20/21-23/24; those in 16/17 and

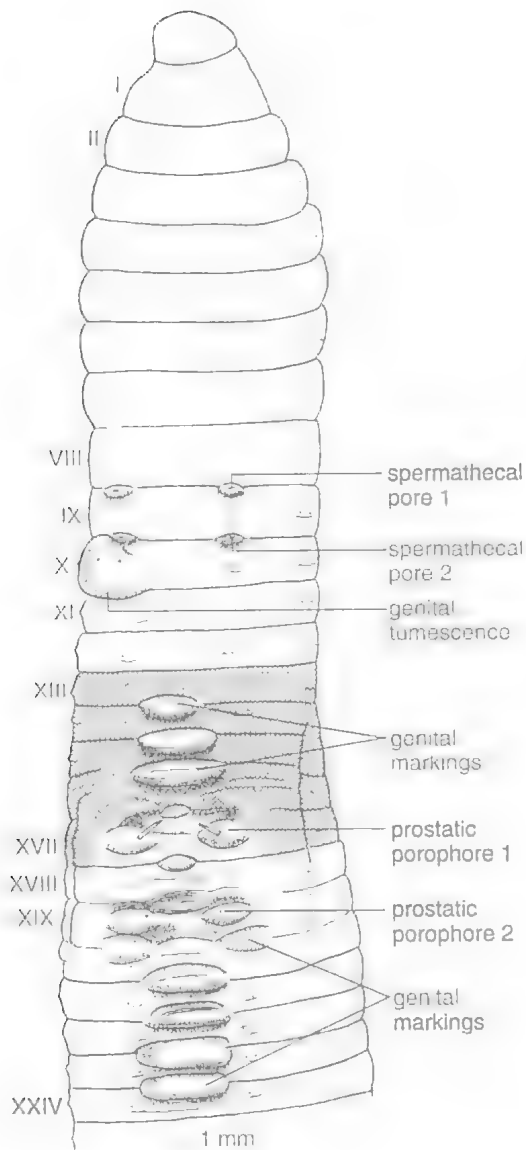


FIG. 1. *Diplotrema acropetra* sp. nov. Holotype, QMG212027. Ventral view of forebody and clitellar region (clitellum drawn from Paratype 1). Note that in this species the spermathecal pores are transposed one segment posterior to the normal megascolecid location.

17/18 small; a suggestion of a pad in 18/19 (H). Female pores not visible. Spermathecal pores 2 pairs, in 8/9 and 9/10 (H); this unusual location being confirmed in P1-9.

Septa 8/9 and 9/10 the thickest, fairly strongly thickened. Dorsal blood vessel single, continuous

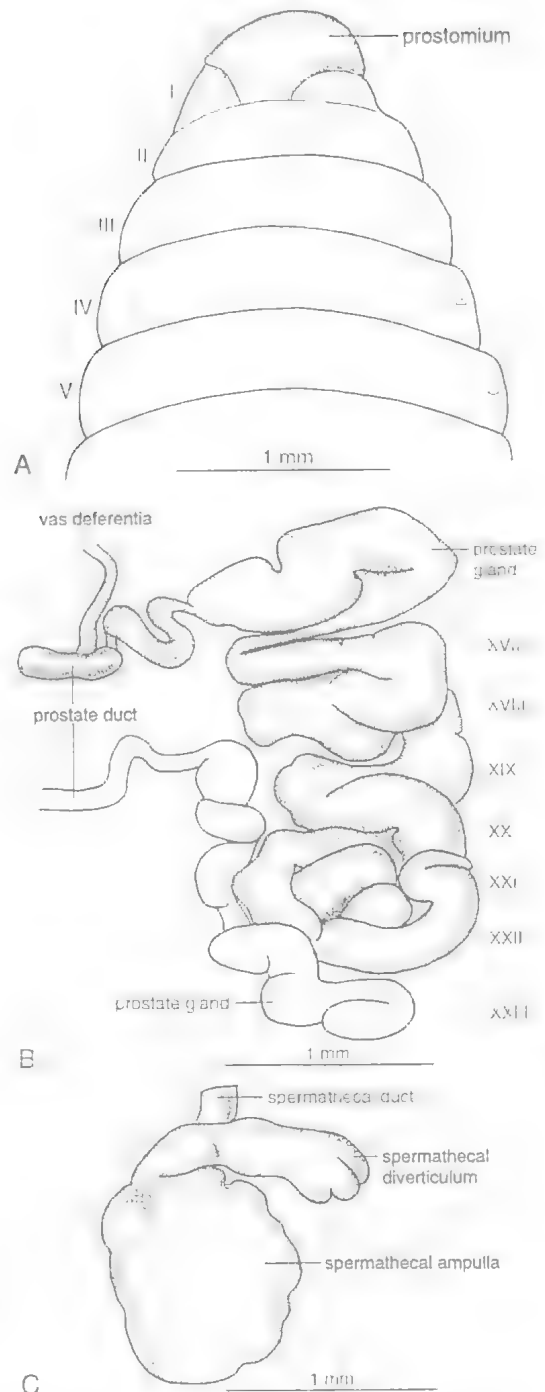


FIG. 2. *Diplotrema acropetra* sp. nov. Holotype, QMG212027. A, dorsal view in region of prostomium. B, right prostates, with penial setae omitted; only the anterior prostate is shaded. C, right spermatheca of IX.



FIG. 3. *Diploptrema acropetra* sp. nov. Holotype, QMG212027. A and B, two right penial setae of XIX. C and D, different views of the tip of seta show in A. E-G, successively more posterior to near basal regions of same.

onto the pharynx. Last hearts in XIII; in XI-XIII stout, laterooesophageal, the connectives to the supraoesophageal vessel being wide, those to the dorsal vessel scarcely apparent; commissurals in X anteriorly slender, with dorsal connectives only. Gizzard very large, an elongate, glossy,

muscular cylinder about three times longer than wide, in V, but its posterior end at the level of segment X. Oesophagus segmentally dilated, and longitudinally compressed, in each of XIV-XVI; the walls in these segments with numerous closely situated, deep, internal lamellae but

lumen not constricted off from that of the oesophagus. Intestine commencing with abrupt expansion in XVIII. Dorsal typhlosome very well developed from about XXIX posteriad. Holonephric throughout; at least two pairs of nephridia anterior to the gizzard are convoluted, not tufted, and each nephridium sends a duct anteriorly to the pharynx. Typical nephridia each with preseptal funnel and slender, avascular duct discharging preseptally in the vicinity of the dorsal setal couples (*cd*). Metandric; large seminal funnels, with spermatozoal iridescence, in XI only. Seminal vesicles racemose, in XII only. Flattened ovaries, with many egg strings, in XIII. Two pairs of thickly tubular prostates, with ectal ducts discharging in XVII and XIX. The anterior pair is very much the larger and winds from XVII to XXII; the tortuous muscular duct is joined near its ectal end by the thick, vas deferens, the width of which, greatly exceeding that of a normal vas, suggests that it is a sperm reservoir. Posterior prostates winding from XIX to XXIII; the ectal duct shorter, though still long, less tortuous and poorly muscularized. Both pairs of prostate ducts overlain by penisetal follicles. Penial setae curved through a right angle or slightly less; the tip widened reflexed 'dorsally' for a short distance before curving 'ventrally' to a V-shaped tip, the tip thus having the appearance of a poised cobra; in frontal view this may give the spurious appearance of a ladle-shape; sculpturing in the midregion consisting of palisades of pointed scales in incomplete circlelets, the circlelets being spaced longitudinally at approximately 10µm intervals; the scales sparser basally; some groups of scales continuing to, but not including, the modified tip; alternatively the scales may form small obliquely arranged groups, each group consisting of a small protuberant semicircle of pointed teeth which overlie a depression, so that the seta resembles a grater; length of a well developed right penial seta 1mm (H). Genital setae present at the tumescences in X or X and XI; each with the usual diplostreman appearance, a stout seta with four opposed longitudinal series of long notches and the tip slightly expanded below the terminal point; the seta gently curved; the longitudinal notches confined to approximately the ectal third; length right seta of IX (measured in a straight line from tip to base) = 0.9mm; greatest width, near base, 60µm. Spermathecae two pairs, transposed

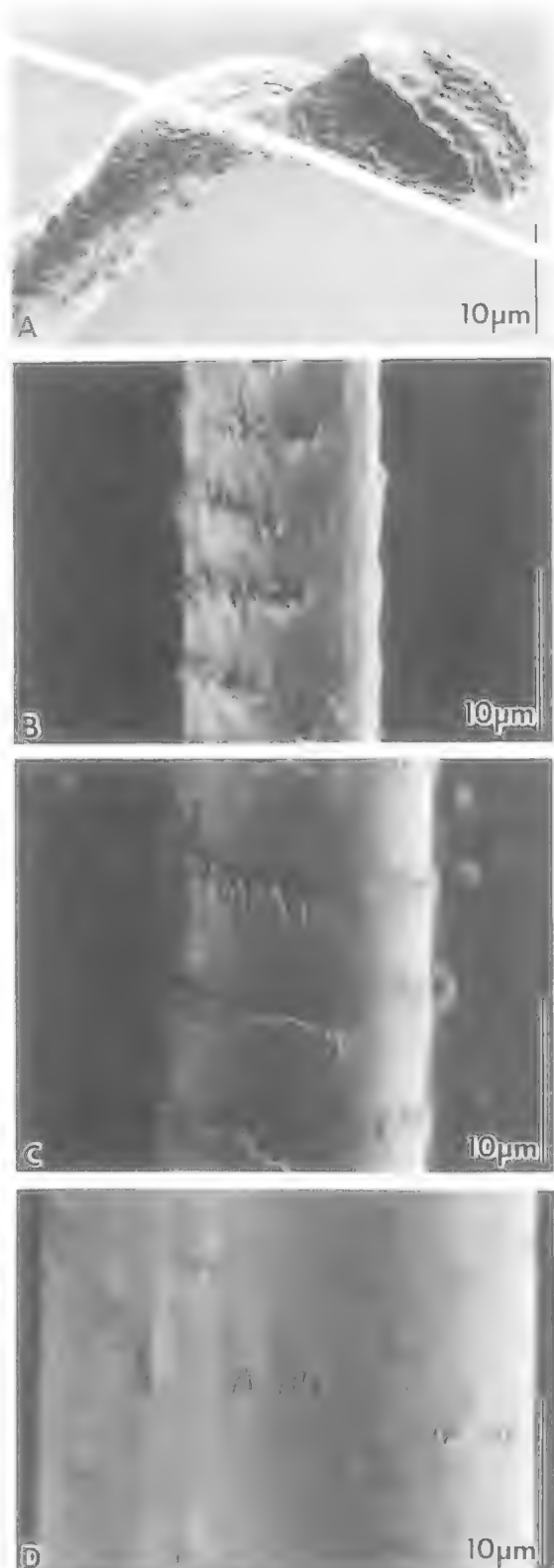


FIG. 4. *Diplostrema acropetra* sp. nov. Holotype, QMG212027. A-D, Tip and successively more posterior regions of a penial seta of XVII.

posteriorly one segment, relative to the usual megascolecoid condition, so that the posterior pair is in X, the anterior pair in IX. The posterior pair of spermathecae, in X, very much larger than the anterior pair; each posterior spermatheca with a sacciform ampulla, a short narrow duct; and a large multiloculate and apically lobed diverticulum, containing sperm bundles, which joins the junction of ampulla and duct and is elongated at approximately a right angle to the duct. Length right spermatheca of X = 1.5mm; length ampulla = 1.0mm; ratio length spermatheca: length duct (including base of diverticulum) = 3.5; length of diverticulum lateral of duct = 0.6mm. The diverticula of the anterior spermathecae are small 'rosettes' of loculi.

**ETYMOLOGY.** From the Greek *acros*, peak, and *petros*, a rock.

**REMARKS.** Transposition of the spermathecae, from the usual position in VIII and IX to IX and X, is unknown elsewhere in *Diplopleura*. This correlates with the unusual slender condition of the commissural blood vessels, and suppression of testes and funnels in X, giving the metandric condition. As the prostatic porophores are in their normal segments of XVII and XIX, it is clearly not due to interpolation of a segment, as occurs in some species of the closely related genus *Acanthodrilus*, in New Caledonia (Jamieson & Bennett, 1979).

Rocky Peak is an isolated upland plateau of Battle Camp sandstone, adjacent to the Deighton Tableland. The swampy habitat is the most northerly location of a habitat type dominated by *Banksia robur*.

***Diplopleura attenuata* sp. nov. (Figs 5-8; 39)**

**TYPE LOCALITY.** Peach Creek, McIlwraith Range, 13°44'17"S 143°20'15" ± 5"E, altitude 500-520m in bank of stream in notophyll vine forest, on Kintore adamellite granite, K.R. McDonald, A.J. Stewart, W.E. Martin, 26 Sep 1995 and, K.R. Mc., A.J. S., 23 Sep 1996.

**MATERIAL EXAMINED.** HOLOTYPE, QMG212000. (Includes microscope slides of left and right anterior penial seta and left genital setae of VIII). PARATYPES. 1-8 QMG212038-45; P9 QMG-212046; P10-12 QMG212019-212021; P13-17 QMG213386-213390; P18-20 QMG211972; P21-23 QMG213402-213404. OTHER MATERIAL. Several not designated types QMG211980, 212022.

**DESCRIPTION.** Length 106-163 (a live specimen 230) mm, H 115mm. Width (midclitellar)

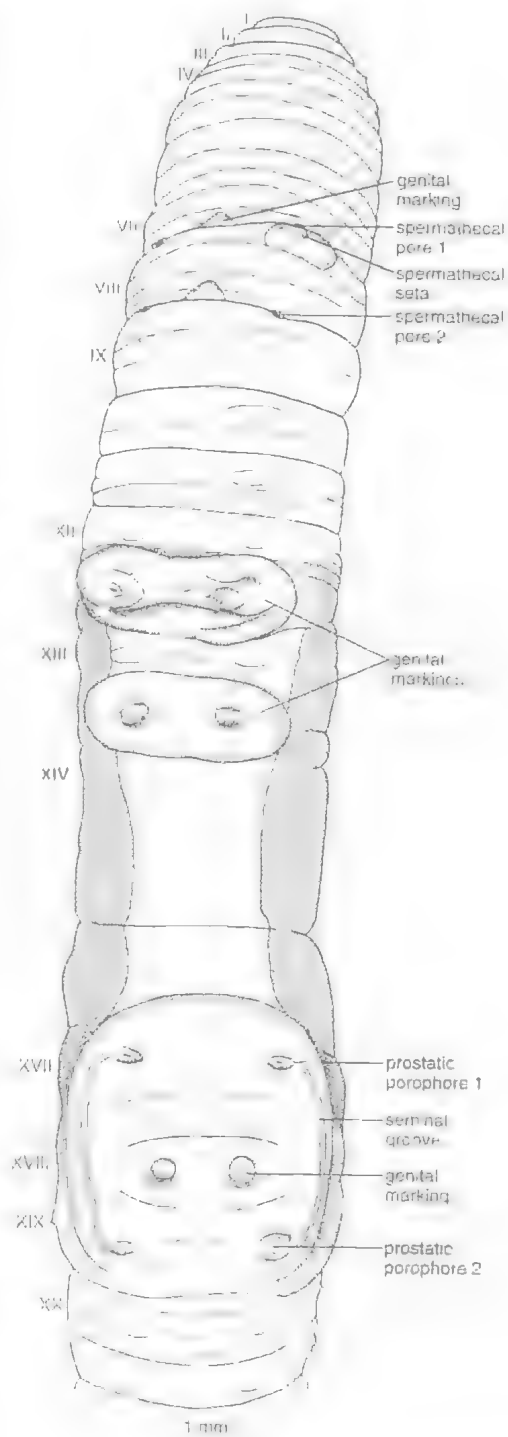


FIG. 5. *Diplopleura attenuata* sp. nov. Holotype, QMG212000. Ventral view of forebody and clitellar region.

2.0- (H) 2.5mm. Segments 140-256, H 155. Uniformly circular in cross-section throughout. Pigmentless buff in alcohol, clitellum, when tumid, pale pink; in life, blood red throughout. Prostomium small, prolobous, slightly indenting the peristomium which is about as long as segment II. Dorsal pores absent. Setae 8 per segment, commencing on II; ventral setal couples absent from XVIII; those of XVII and XIX modified as enlarged penial setae; genital setae present in VIII, with the usual diplotreman ornamentation consisting of notches. *aa: ab: bc: cd: dd* = 4.8: 1.0: 4.3: 0.8: 11.6; = 16.8: 3.5: 15.1: 17.9: 40.5%. Nephropores not visible. Clitellum well-developed, saddle-shaped, extending over 1/2XII-XVII, with a midventral gap that extends to, or slightly beyond, *b* lines. Male pores not visible. Prostatic pores 2 pairs, in XVII and XIX, each pore on a minute oval papilla which is equatorial and slightly lateral of *b* lines relative to adjacent segments; the papillae of a side linked by a weakly developed slightly parenthesis seminal groove; the entire male genital area forming a raised, almost square area, slightly longer than wide, with rounded vertices. Genital markings: a broad, unpaired midventral pad extending laterally beyond *b* lines, intersegmental in 10/11 (P1, P3, 4, 6-9), 11/12 (P8), 12/13 (H, P2), 13/14 (H, P2), 14/15 (P2) but extending almost to the setal arcs of each adjacent segment; each pad bearing a pair of approximately hemispheroidal papillae median of *a* lines; highly diagnostic is a similar pair of papillae, on a less distinct transversely oval area, segmentally situated on XVIII (all specimens); a transverse segmental pad frequently present in XX (P1, 3, 6-9). Further markings a midventral postsetal triangular slight tumescence in VII and VIII (H, P2, 6, 7, 9). An unpaired oval-rectangular genital tumescence on the left side straddling and extending beyond *ab*, in the anterior half of VIII, with two punctuations representing genital setae. Female pores small transverse slits presetally in *a* (P1) or *b* (H) lines. Spermathecal pores 2 pairs, in 7/8 and 8/9, slightly lateral of setae *b*; inconspicuous but definite orifices visible by parting the intersegment (H, P1-9).

Septa 5/6-8/9 strongly thickened, the last two the thickest. Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XIII; those in X-XIII, latero-oesophageal, with connectives to the dorsal and supraoesophageal vessels; commissurals in IX anteriorly slender, not heart-like, though in IX, at least, possibly latero-oesophageal. Gizzard small, compressible though with

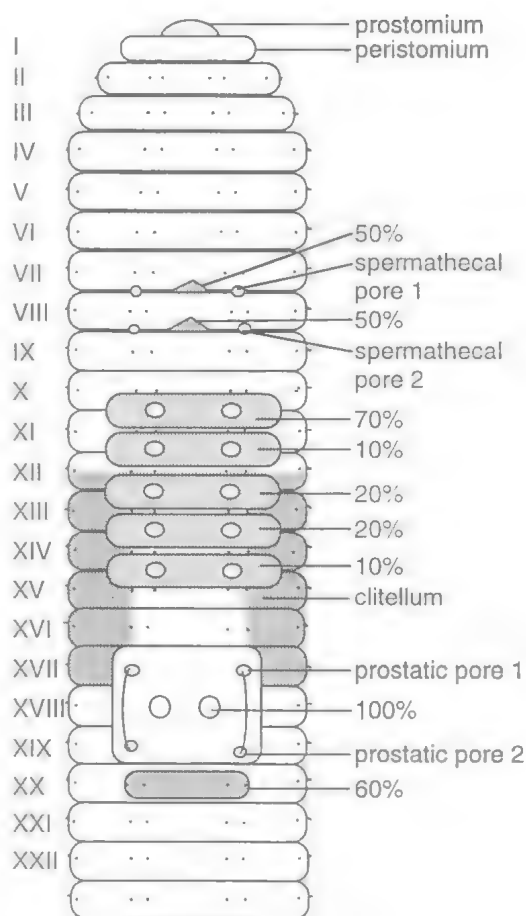


FIG. 6. *Diploptrema attenuata* sp. nov. Diagram showing distribution of genital markings in the holotype and 9 paratypes.

some muscular sheen, almost vestigial, in V. Oesophagus suppressed in VI by backward extension of septum 5/6; segmentally slightly swollen, and vascularized in VII to IX; a simple tube from X(?), XI to 1/2XIX in which the intestine commences with abrupt expansion; typhlosole absent. Ventrolateral masses in XIII give the spurious impression of calciferous glands but are not connected to the oesophagus and disintegrate on manipulation. Holonephric throughout; nephridia not seen in a few anterior segments and no tufting detected; nephridia with preseptal funnel near nerve cord and slender duct discharging in line with the dorsal setal couples (*cd*); caudally the body of the nephridium has the appearance of a convoluted sac but bladders are absent. Holandric; large sperm masses, and very large iridescent sperm funnels free in X and XI. Two pairs

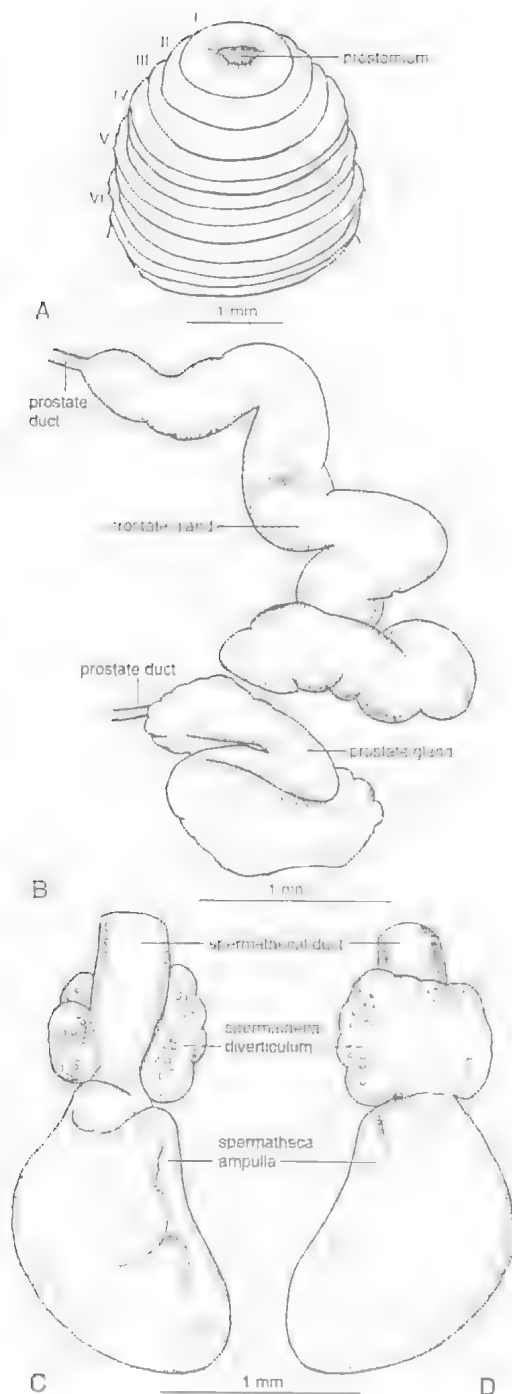


FIG. 7. *Diplotrema attenuata* sp. nov. Holotype, QMG212000. A, dorsal view in region of prostomium. B, right prostates, with penial setae omitted. C and D, ventral and dorsal views of the left spermatheca of IX.

of large, racemose seminal vesicles which fill the length of their segments, in XI and XII. Moderately large, flattened bushy ovaries, and funnels, in XIII; small, multichambered, berry-like masses on each side of the oesophagus in XIV are presumably ovisacs. Prostates two pairs, with ducts discharging in XVII and XIX; those in XVII considerably the larger and with the form of tortuous thick tubes which end in XVIII; those in XIX flattened and strap-like in their midregion, and approximately S-shaped; each prostate with a short slender duct which is obscured by the large penisal follicles. Male genital field of XVII-XIX represented internally by diffuse glandular modification of the body wall but no bursae present. Paired, conjoined vasa deferentia with closely adpressed bends, and spermatozoal iridescence, traced on each side to immediately behind the ectal end of the duct of the anterior prostate, but termination not seen. Penial setae strongly curved throughout their lengths; the tip not widened, reflected dorsally or not and ending bluntly in a rounded swelling with a pitted surface; sculpturing (best developed in the mid-region) consisting of pointed scales, contiguous side by side, in incomplete circlelets; the circlelets spaced longitudinally at approximately  $15\mu\text{m}$  intervals; the scales stopping short of the modified tip near which they are in small groups rather than circlelets; length of a well developed right penial seta  $1.3\text{mm}$  (P10). Genital setae present at the tumescences in VIII; each with the usual diplotreman appearance, a stout seta with four opposed longitudinal series of long notches and the tip slightly expanded below the terminal point; length left seta  $=0.5\text{mm}$  (incomplete?); greatest width, near base,  $=25\mu\text{m}$ . Spermathecae 2 pairs, the posterior somewhat the larger, each with a large irregularly ovoid ampulla and straight broad, well demarcated muscular duct of about half its length; a multiloculate diverticulum, with a form reminiscent of a clenched fist, sessile dorsally on the duct at the junction of the latter with the ampulla, the few main loculi being laterally situated and filled with innumerable very small, iridescent sperm balls; length left spermatheca of IX  $=2.3\text{mm}$ ; length ampulla  $=1.4\text{mm}$ ; ratio length spermatheca: length duct  $=2.6$ ; greatest dimension of diverticulum (transversely)  $=0.8\text{mm}$  (H).

**ETYMOLOGY.** Named for its unusually attenuated form.

**REMARKS.** The genital field, particularly the two knob-like genital markings median to the

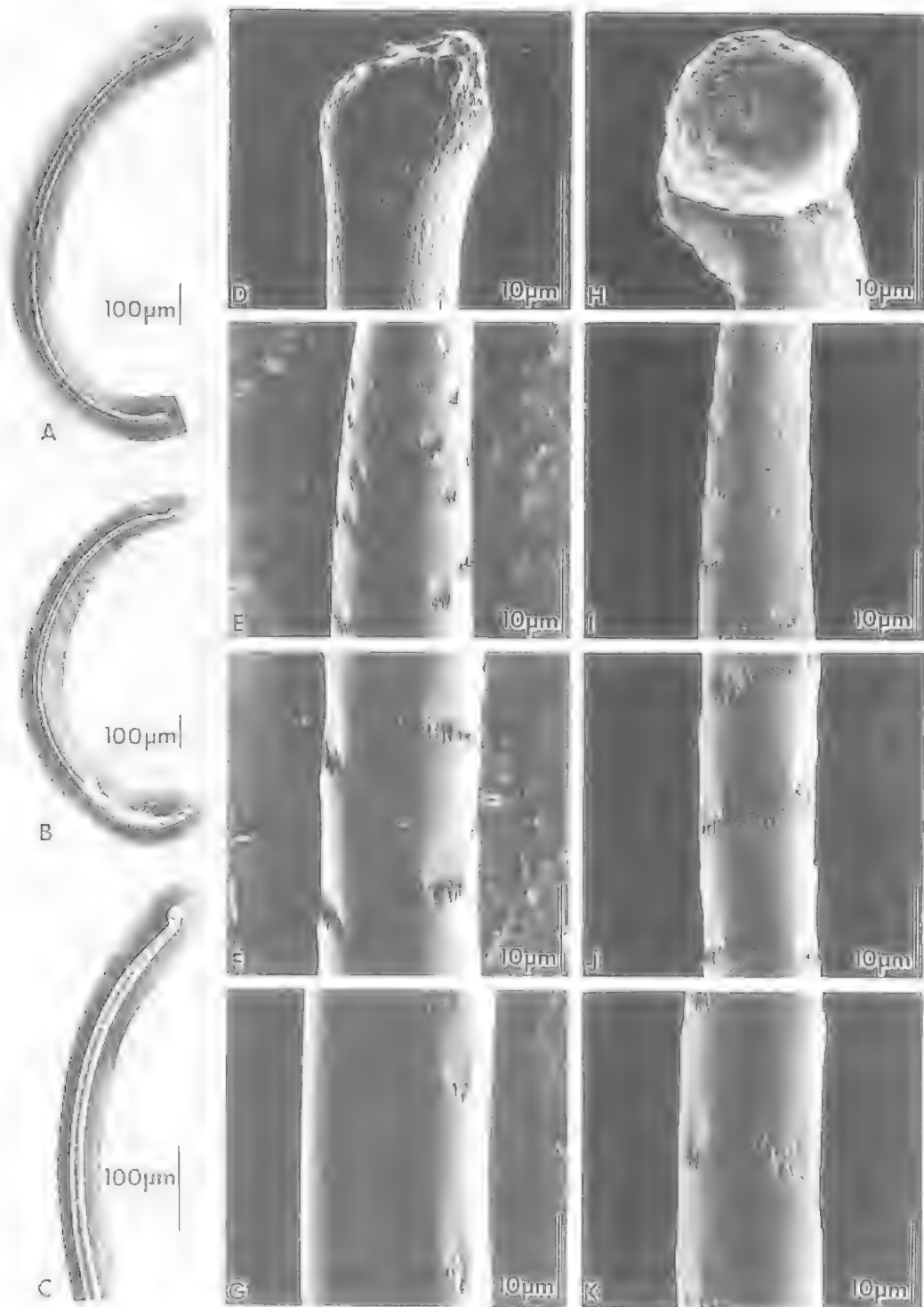


FIG. 8. *Diplotrema attenuata* sp. nov. Paratype 10, QMG212019. Scanning electron micrographs. A, a right penial seta of XVII. B and C, a right penial seta of XIX. D-G, appearance of seta shown in A from the tip to near the base. H-K, same for seta shown in B and C.



seminal grooves on segment XVIII, is diagnostic of *D. attenuata*. The male genital field of this species, when fixed, is emphasized by the fact that the body is almost always dorsally arched anteriorly and posteriorly to it. The body is also contorted elsewhere.

The absence of dorsal pores is attributable to an amphibious existence in earthworms. It is unknown in other published species of *Diplopleura* with the exception of *D. cornigravei* (Michaelsen, 1907) and possibly *D. macleayi* (Fletcher, 1890), both inadequately described species from Western and North Western Australia, respectively.

***Diplopleura scheltingai* sp. nov.**  
(Figs 9-11; 39)

**TYPE LOCALITY.** 13°44'17"S 143°20'15"E, Peach Creek, McIlwraith Range, altitude 500-520m. In moist upper root horizon down to about 25cm, notophyll vine forest with fan and feather palms, stream bank, sandy loam, on Kintore adamallite granite. K.R. McDonald, A.J. Stewart, 25-27 Sep 1996.

**MATERIAL EXAMINED.** HOLOTYPE. QMG212001 (includes microscope slide of left genital seta of VIII). PARATYPES. P1 & 2 QMG212003-212004; P3 QMG211981; P4 QMG213401; P5 QMG213406.

**DESCRIPTION.** Length 74 (H)-104 (P3)mm. Width (midclitellar) 5mm (H, P3). Segments 188 (P3)-204 (H). Uniformly circular in cross-section throughout, pigmentless buff in ethanol, including clitellum. Prostomium prolobous but deeply indenting the peristomium dorsally; peristomium longer than segment II; first dorsal pore in 11/12 but not definitely perforate until 17/18. Setae 8 per segment, commencing on II; in XII, *aa: ab: bc: cd: dd* = 5.0: 1.0: 4.8: 1.0: 21.4; or 12.5: 2.5: 12.1: 2.4: 53.5%; ventral setal couples of XVIII absent; those of XVII and XIX modified as enlarged penial setae; setae *a* and *b* of VIII forming genital setae. Nephropores visible in the postclitellar body, a pair in each segment, each pore a faint spot anterior to each seta *b*. Clitellum well-developed, extending over XII-XVII, interrupted ventrally by the male field in XVII, with doubtful midventral development anterior to the field (H), or interrupted between the ventral setal couples throughout, i.e., saddle-shaped (P1-3). Male pores not visible. Prostatic pores 2 pairs, in XVII and XIX, each pore on a minute oval papilla which is in line with the ventral setal couple (*ab*) of adjacent segments; the papillae of a side linked by a parenthetic seminal groove; the pore accompanied by one or more minute punctuations pre-

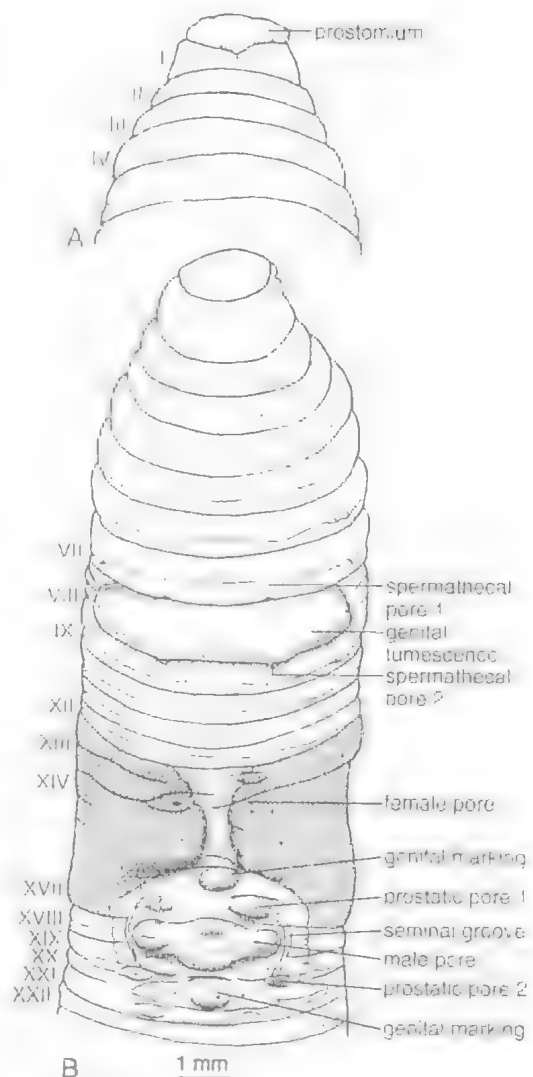


FIG. 9. *Diplopleura scheltingai* sp. nov. Holotype, QMG212001. A, dorsal view in region of prostomium. B, ventral view of forebody and clitellar region.

sumably representing penial setae, but the latter not protuberant; the posterior end of each seminal groove continuous onto a small transversely elliptical papilla which is centred lateral to *b* lines at the posterior limit of XIX; the male genital area depressed relative to the anteriorly bounding clitellum. Genital markings: a pair of rounded papillae in *ab* of XVIII, filling the segment longitudinally, the summit of each with a pore-like marking which from internal examination appear to be the male pore. The two papillae connected

by a prominent transverse bar which is widened midventrally so as to impinge strongly on segments XVII and XIX, the widened region bearing a median elliptical protuberance (H, P1-3). Further genital markings a small transversely elliptical pad anterior to the prostate pores of XVII (H, P1) and a similar pad in XX with tumid lateral extensions which include the ventral setal couples (H, P1, P3). A strongly protuberant genital tumescence in VIII fills, and expands the segment longitudinally, and takes in seta *c* on each side (H, P1-3); genital setae present. Female pores a pair of small transverse slits, each with narrow border, presetally slightly lateral of *a* lines of XIV (H). Spermathecal pores 2 pairs, in 7/8 and 8/9, in or very slightly lateral of setae *a*; inconspicuous but definite orifices, closely apposed to the genital tumescence.

Septa 7/8-12/13 strongly thickened; 9/10-11/12 slightly thickened. Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XIII; those in X-XIII, latero-oesophageal, with connectives to the dorsal and supraoesophageal vessels. Gizzard very large, an elongate, glossy, muscular, cylinder; in V. Oesophagus lacking calciferous glands; but very wide and vascular, without intersegmental constriction, in XVI and XVII (H, P1). Intestine commencing, with abrupt expansion, in XX; a very large dorsal typhlosole commencing in XXII-XXIII, consisting of two distinct laminae (H, P1). Holonephric, a large nephridium present on each side throughout but in caudal segments several longitudinal zigzagged ducts are present on each side running from one segment to the next; tufting absent. Holandric; testes, large sperm masses, and very large iridescent sperm funnels free in X and XI. Seminal vesicles racemose, in IX and XII; similar in size in the two segments (H, P1). Small ovaries, with few egg strings, in XIII. Somewhat flattened tubuloracemose prostates, two pairs, in XVII and XIX, restricted to these segments; those in XIX considerably larger than those in XVII (H), or the anterior pair slightly larger (P1); each gland folded on itself at least twice, and, especially

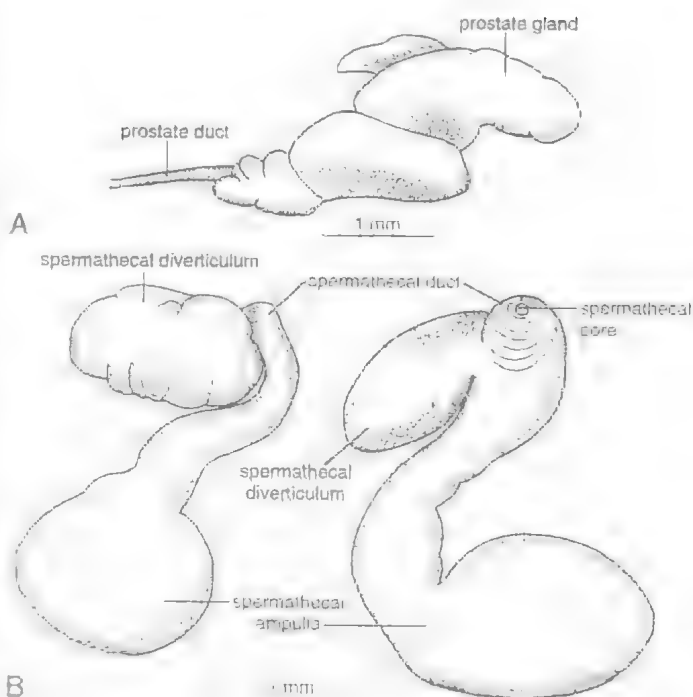
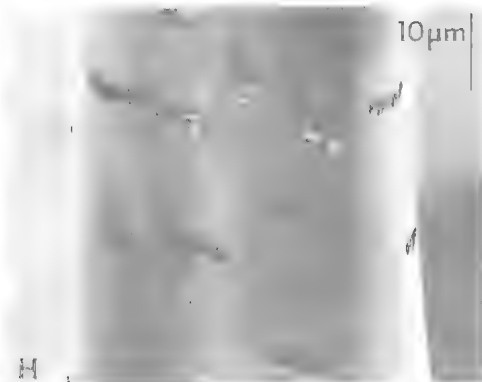
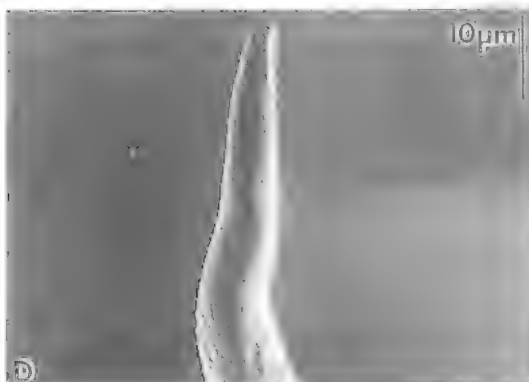
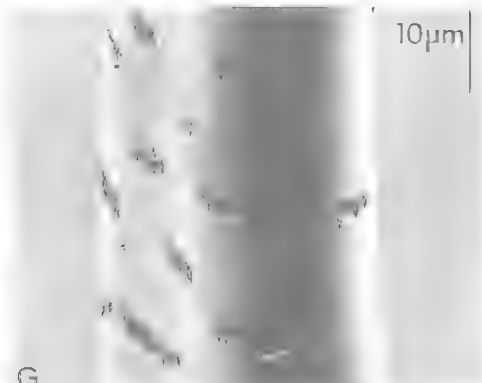
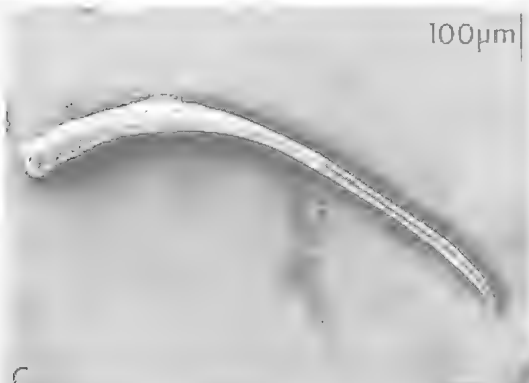
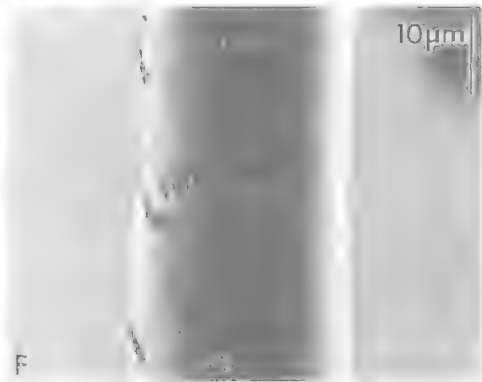
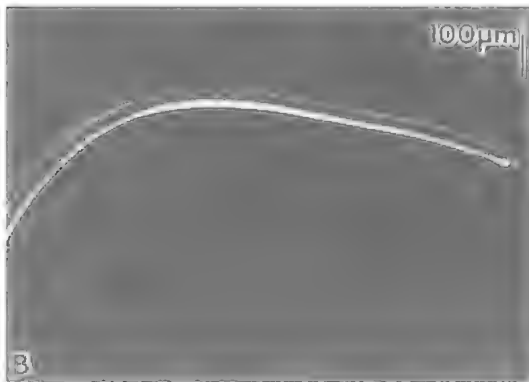
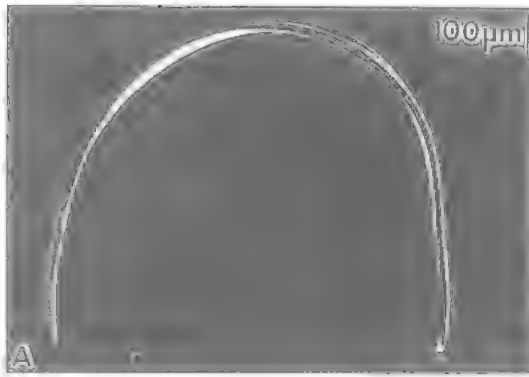


FIG. 10. *Diplotrema scheltingai* sp. nov. Holotype, QMG212001. A, right prostate of XIX. B, approximately dorsal and ventral views of right spermatheca of IX.

ectally, incised, so as to appear racemose; a narrow central lumen present but the surrounding glandular tissue very thick; the duct moderately long, and slender, medianly directed, and accompanied by two large follicles of penial setae (H, P1). The duct of each anterior prostate (examined closely in the holotype) discharges at a large bursa median to which is a smaller bursa associated with the penisetal follicles. The larger bursa overlies a more posteromedian smaller bursa, in XVIII, into which discharge the two thick, conjoined vasa deferentia of its side, these curving medianly in a wide arc. The posterior prostate ducts do not appear to terminate at bursae but there are internal protrusions of the body wall near the point of entry of the penisetal follicles into the body wall (H). Penial setae curved through from 30° to 180°, the tip tapering to a smooth, simple point and bent to a varying extent; sculpturing consisting of many unevenly spaced

FIG. 11. *Diplotrema scheltingai* sp. nov. Holotype, QMG212001. Scanning electron micrographs. A-C, two right penial setae of XIX. D, Tip of C. E-H, appearance of seta shown in A and B from the tip to near the base.



groups each of several contiguous pointed teeth; near the tips the groups are extensive circumferentially at fairly regular longitudinal intervals of approximately  $1.7\mu\text{m}$  (H). Genital setae, in VIII, gently curved but a short basal region more strongly curved in the same direction; more slender relative to length than usual for *Diploptrema* but with the usual longitudinal notching and expansion of the tip below the terminal point; length (straightened) =  $1.8\text{mm}$ ; greatest width, near base, =  $51\mu\text{m}$  (H). Spermathecae 2 pairs, in VIII, and IX, the posterior pair slightly the larger; each with an ovoid ampulla and longer, slender fairly well demarcated duct which is joined near its swollen ectal end by a large, ellipsoidal, multiloculate diverticulum containing many minute iridescent balls of sperm; length left spermatheca of VIII =  $2.6\text{mm}$ ; length ampulla =  $1.1\text{mm}$ ; ratio length spermatheca: length duct =  $1.7$ ; greatest dimension of diverticulum =  $0.9\text{mm}$ .

**ETYMOLOGY.** Named for my colleague and friend, David Scheltinga.

**REMARKS.** The tripartite transverse bar on segment XVIII is distinctive of *D. scheltingai*. The fact that the nephridia, though apparently only one pair per segment (preservation being inadequate for certain determination of their condition), have multiple longitudinal ducts possibly merits placement of this species in *Neodiploptrema*. The validity of separating *Neodiploptrema* from *Diploptrema* is uncertain as it is possible that the meronephric condition of the latter taxon has evolved more than once from the holonephric *Diploptrema* condition.

#### Genus *Neodiploptrema* Dyne, 1996

The definition of *Neodiploptrema* as recently defined by Dyne (1996) differs from that of *Diploptrema* only in the description of the excretory system: 'Meronephric, avesciculate; anterior tufted nephridia present'. It is shown below that tufted nephridia may be absent.

The three new species, *Neodiploptrema altanmoui*, *N. mcdonaldi* and *N. paripunctata*, represent a significant extension of the known range of the genus to the east of the northern continuation of the Great Dividing Range. Previously the genus was known only from monsoonal semi-deciduous vine forests in the Lockerbie, Iron Range and Weipa areas, and Thursday Island (Dyne, 1996), that is western or northern flowing catchments at the tip of the Cape York Peninsula.

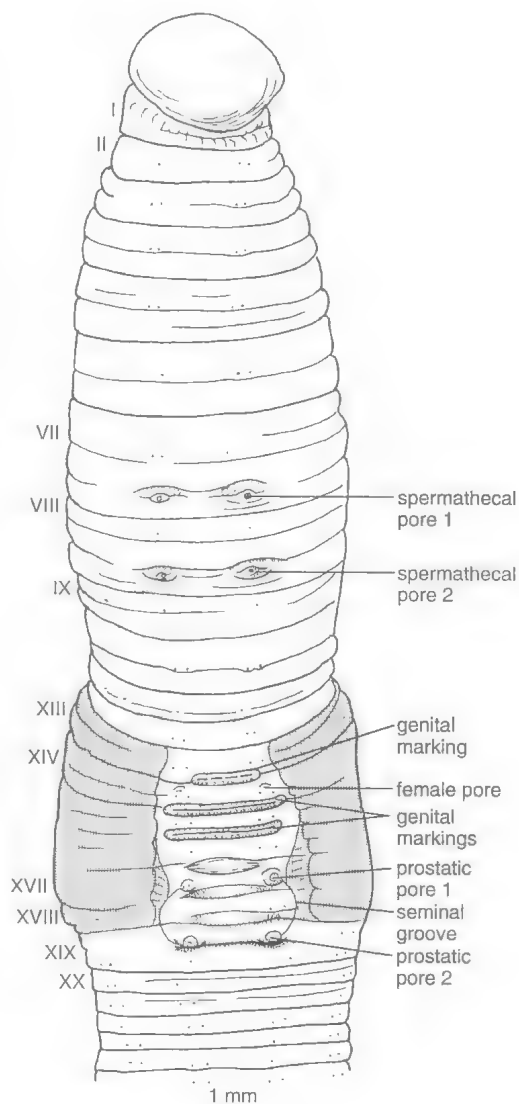


FIG. 12. *Neodiploptrema altanmoui* sp. nov. Holotype, QMG21 1986. Ventral view of forebody and clitellar region.

In the newly demonstrated localities the genus is sympatric with *Diploptrema*.

#### *Neodiploptrema altanmoui* sp. nov. (Figs 12-16; 39)

**TYPE-LOCALITY.**  $14^{\circ}33'31''\text{S}$   $144^{\circ}38'08''\text{E}$ , Altanmoui Section, Cape Melville National Park, alt. 560-570m, vine forest on sandstone escarpment, under logs and rocks on forest floor, K. McDonald, P.J. Lethbridge, 8 Apr 1995. Formalin fixation.

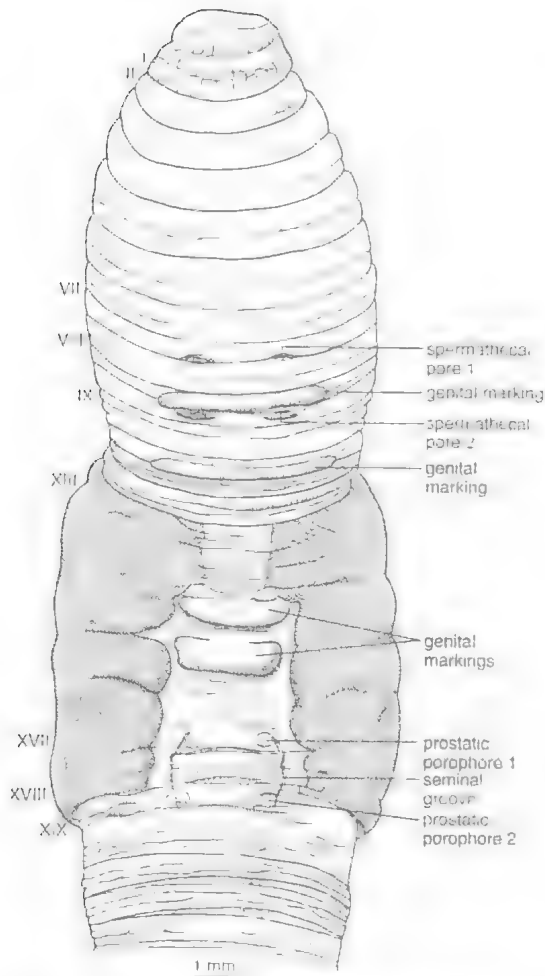


FIG. 13. *Neodiploplectura altanmouli* sp. nov. Paratype 3, QMG211987. Ventral view of forebody and clitellar region.

MATERIAL EXAMINED. HOLOTYPE. QMG211986. PARATYPES. P1 and 2 QMG212023.

Same data, in mesophyll vine forest, under rock, Paratype 3 QMG211987.

**DESCRIPTION.** Length 140mm. Width (mid-clitellar) 7.6mm. Segments 258 (H). Circular in cross-section, pigmentless in alcohol. Prostomium wide and prolobous but a suggestion of a narrow continuation onto the much fissured peristomium, a middorsal groove being wider than the others (H, P3). First dorsal pore 12/13 (H, P3). Setae 8 per segment, in regular longitudinal rows throughout; ventral seta couples of XVIII present; those of XVII and XIX modified as enlarged penial setae; no genital setae (H, P3); in XII, *aa*:

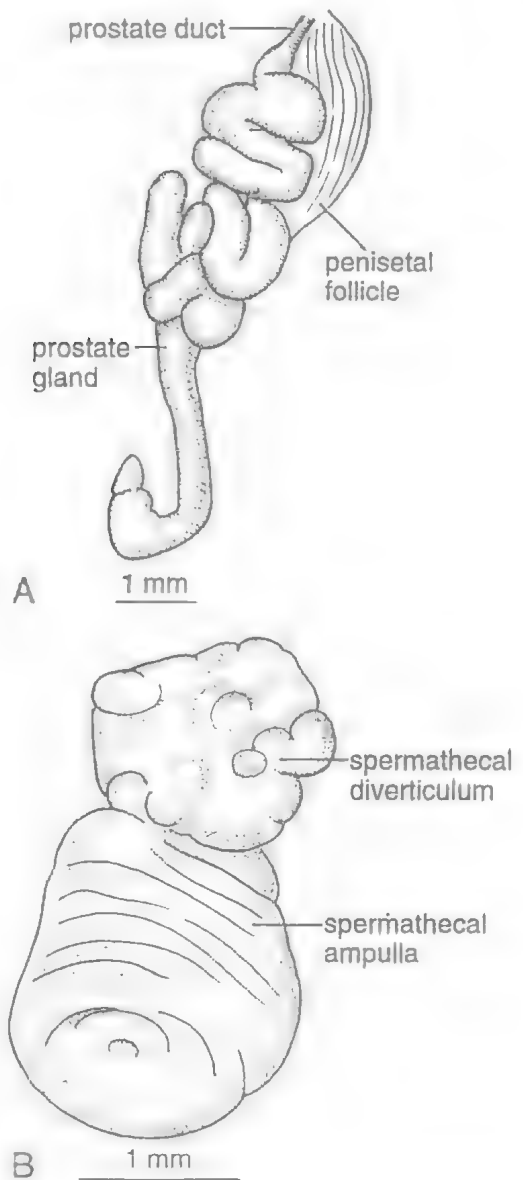


FIG. 14. *Neodiploplectura altanmouli* sp. nov. Paratype 1, QMG212023. A, right prostate of XIX. B, right spermatheca of IX.

*ab*: *bc*: *cd*: *dd* = 6.3: 1.0: 7.1: 1.0: 48.3; or 8.7: 1.4: 9.8: 1.4: 66.4% (H). Nephropores sporadically visible as a transverse series of minute ovals anteriorly in their segments. Clitellum saddle-shaped, protuberant, over XIII-XVIII; ventral margins well above *b* lines (H, P3). Prostatic pores 2 pairs, in XVII and XIX, coincident with the penial seta orifices, in *ab*, on small subcircular

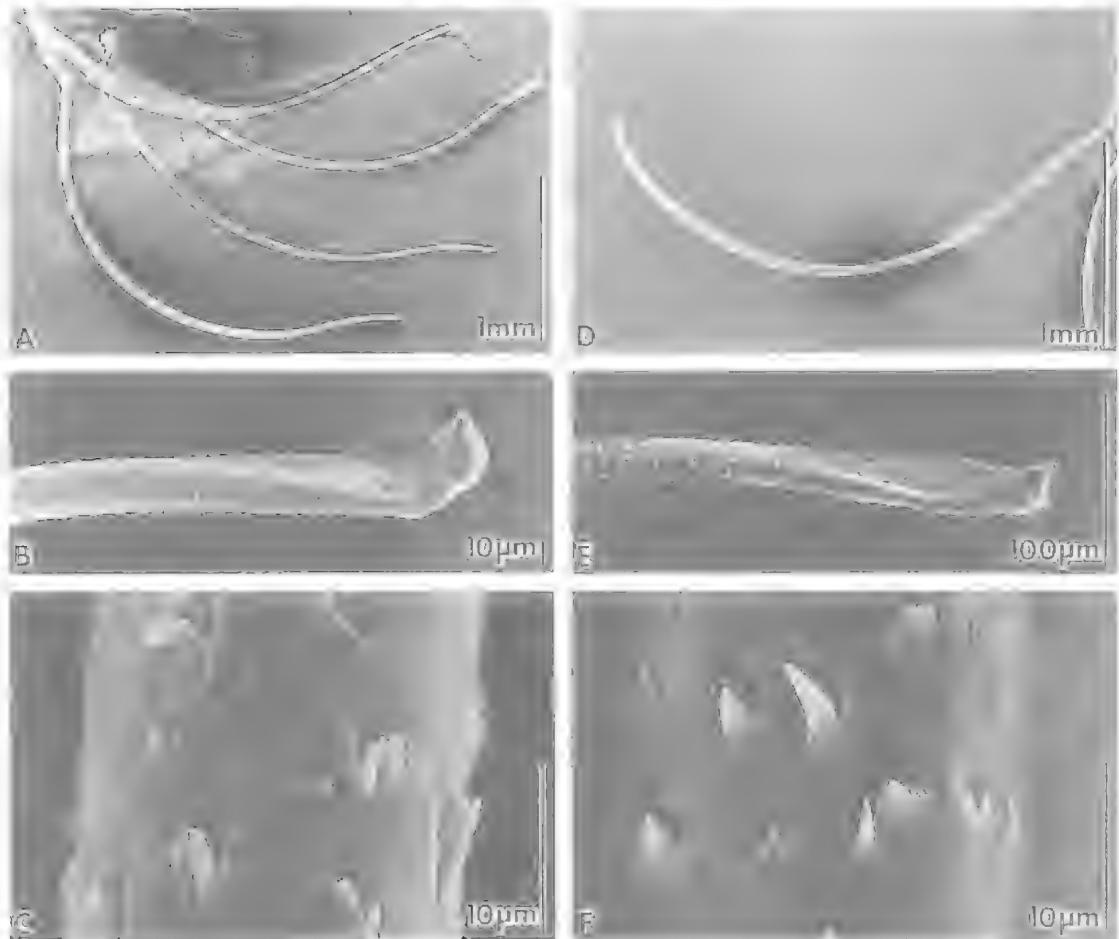


FIG. 15. *Neodiploptrema altanmoui* sp. nov. Holotype, QMG211986. Scanning electron micrographs. A, right penial setae of XVII. B, ectal region of a penial seta. C, detail of sculpturing of same. D, penial setae of XIX. E, ectal region of a penial seta of XIX. F, detail of sculpturing of same.

porophores; seminal grooves, joining the prostatic porophores of a side, forming parentheses with their midpoint, and presumably the male pores, lateral of *b* lines at the equator of XVIII (H, P3), the grooves deeply incised in P3, faint (owing to maceration?) in H; the anterior prostate pores 2.3mm, ca. 0.1 body circumference apart (H). Genital markings indefinite in the macerated holotype, whitish somewhat keratinized-looking transverse unpaired midventral ridges in intersegments 13/14, 14/15 and 15/16 (the most pronounced), XX and XXI, including the ventral setal couples; clearly visible in the better preserved P3 in which they consist of a narrow ventral band or pad posterior in each of VIII and X and extending well laterally of *b* lines, with their anterior borders at but not including the setal

arc; that in VIII posteriorly abuts closely on the spermathecal pores of 8/9; other markings two much larger but transversely less extensive pads one at each of intersegments 14/15 and 15/16 extending shortly lateral of *b* lines, each abutting the ventral setal couples of the previous segment but posteriorly not reaching the following setal arc. Female pores minute transverse slits, each with a crescentic anterior border, immediately anterior to the ventral setal couples, almost in *b* lines (H). Spermathecal pores 2 pairs, in 7/8 and 8/9, in *ab*, definite pores filled with coagulum and with anterior and/or posterior crescentic lips; those of each pair conjoined by a narrow band medianly.

Septa 5/6-10/11, especially 8/9 and 9/10, strongly thickened. Dorsal blood vessel single,

continuous onto the pharynx; last hearts in XIII; those in X-XIII latero-oesophageal, with well developed connectives to the supraoesophageal vessel and much thinner connectives to the dorsal vessel; commissurals in IX and anteriorly slender with dorsal connectives only. Gizzard large, stoutly cylindrical, firm and muscular in V. Oesophagus lacking calciferous glands; transition from oesophagus to intestine indefinite in terms of appearance of the gut wall and presence of fine, silty contents, but not widening until XX (P2, 3); a low, narrow dorsal typhlosole commencing behind the prostates (P1, 3), Meronephric throughout, nephridia commencing in II; very conspicuous, profusely divided tufts present in III and IV, very large and restricted to IV in P3, a thick duct of each tuft running anteriorly, to the wall of the buccal cavity. In the midbody, shortly behind the prostates, approximately 8 astomate micromeronephridia on each side and a median, not especially enlarged but more convoluted, meronephridium for which a preseptal funnel was demonstrated sporadically. Caudally (P2), the medianmost nephridium is greatly enlarged relative to those lying more laterally and has a conspicuous preseptal funnel. Holandric; seminal funnels large in X and XI, only those in XI with spermatozoal masses and iridescence and accompanied on the anterior septum by extensive masses of rounded testicular follicles; in X, funnels lacking spermatozoal iridescence and testes not recognizable (H, P1) but in P2 and P3 there are sperm masses, and funnels are iridescent, in X and XI. Racemose seminal vesicles in IX and XII, those in XII the larger and visible dorsally (H, P3). Bushy ovaries with few oocytes, in XIII (P2) or large, undulating laminae with many oocytes (P3). Prostatic glands two pairs of simple, much convoluted tubular organs; both pairs extending back into XXV; the anterior pair somewhat longer than the posterior pair but both pairs well developed; or the anterior pair in XVII and XVIII, the posterior pair in XIX and XX (P3); each with a short slender, slightly muscular duct (P1); or the glands restricted to segments XVII and XIX (H). Penial setae with two posteriorly joined muscular follicles on each side, each containing two setae, presumably corresponding to *a* and *b* follicles, at each prostate duct; length of a well developed setae (measured in a straight line from base to tip) = 1.9mm. The setae bowed

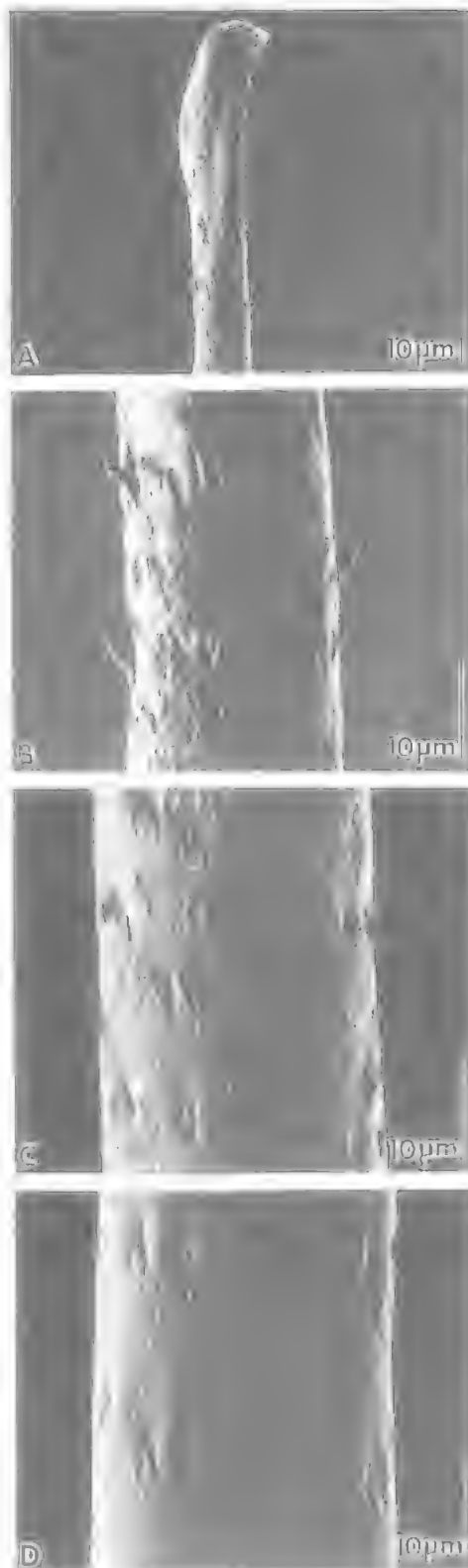


FIG. 16. *Neodiploptrema altanmoui* sp. nov. Right anterior penial seta of paratype 3, QMG211987. A, tip of seta. B-D, progressively more posterior regions of the anterior ornamentation.

through varying degrees, maximally about 90°; the ectal region of the shaft ornamented with circumferential rows of single- or multiple-pointed ectally directed teeth; the tooth rows closely spaced along the seta, approximately 10µm apart; cross section of the seta circular excepting at the tip which forms an elongate spatula, only slightly concave, with thickened margins, and a knoblike, pointed tip; scattered teeth continuing into the spatulate region; the latter sometimes bent 'dorsoventrally', possibly because of compression during copulation. No notable difference in form observed between setae of XVII and XIX (P2); setae of P3 closely similar but with more protuberant thorn-like scales. Spermathecae 2 pairs, in VIII and IX, each organ consisting of a rounded diverticulum sessile on the body wall and obscuring beneath it all but a small ental region of the wide duct and a large saclike ampulla which in the holotype has a series of encircling annuli or pliae; the margins of the diverticulum irregularly and indistinctly lobed owing to many internal sperm chambers (H, P1, 3); in IX, length right spermatheca = 3.3mm; length ampulla 2.0mm; ratio length spermatheca: length duct (with superior diverticulum) = 2.5 (P1).

ETYMOLOGY. After the type-locality.

REMARKS. The *N. altanmoui* specimens were located in moist mesophyll vine forest on the Jurassic Dalrymple sandstone and moist soil where the sandstone escarpment boundary met the Permian Altanmoui granites. It occurs at the headwaters of Wakooka Creek, an eastwards flowing coastal stream arising in the Altanmoui Range. The feather palm forest along drainage lines was dominated by *Archontophoenix* sp. and at an altitude of 540 metres is the highest of this vegetation type in the Laura basin (Cooktown to Princess Charlotte Bay) by a large margin (K.R. McDonald citing J.P. Stanton pers. comm.).

*N. altanmoui* resembles the sympatric *N. paripunctata* and *N. exigua* Dyne, from Lockerbie East, and differs from all other known species of the genus in having seminal vesicles in segments IX (in addition to those in XII). It differs from *N. exigua* in the lobed multiloculate spermathecal diverticulum whereas the latter species has a saciform, blunt diverticulum and in the more anterior origin of the intestine. The male genital field was not developed in *N. exigua*. *N. al-*

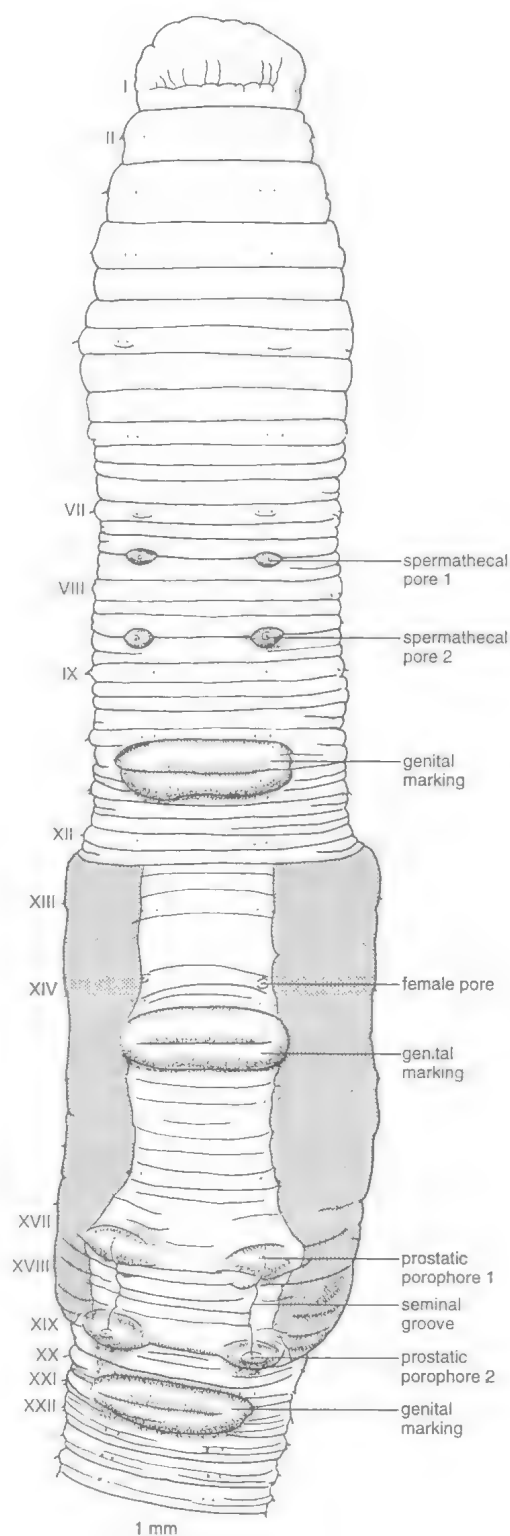


FIG. 17. *Neodiploptrema mcdonaldi* sp. nov. Holotype, QMG212005. Ventral view of forebody and clitellar region.



*tanmoui* further resembles *N. paripunctata* in the form of the spermathecae, with a rosette-like arrangement of loculi of the spermathecal diverticulum on the short spermathecal duct. Differences from the latter species are numerous and include the distinctive setal ratios, the strong denticulation of the penial setae, and the absence of the paired, apposed genital markings posteriorly in XV.

***Neodiplotrema mcdonaldi* sp. nov.**  
(Figs 17-19; 39)

**TYPE LOCALITY.** 13°44'17"S 143°20'15"E  $\pm$  5", Peach Creek, McIlwraith Range, alt. 500-520m. In creek bank, in pig diggings and/or in moist upper root horizon, Notophyll vine forest with fan and feather palms, on Kintore adamallite granite, K.R. McDonald, A.J. Stewart, 23-27 Sep 1996.

**MATERIAL EXAMINED.** HOLOTYPE, QMG212005. PARATYPES. P1-4 QMG212006-212009; P5 QMG212010 (includes microscope slide of left posterior penial seta); P6 & 7 QMG212011-212012; P8 QMG212013; P9-12 QMG212014-17; P13 QMG212018.

**DESCRIPTION.** Length 91-134mm, H 112mm. Width (midclitellar) 4.6-5.0mm, H 4.9mm. Segments 139-264, H 210. Circular in cross-section throughout. Pigmentless pale brownish grey in ethanol. Prostomium more than half the width of the peristomium; prolobous; first dorsal pore in 10/11 (H) or 12/13 (P2); peristomium shorter than segment II. Setae 8 per segment, commencing on II, in XII, *aa: ab: bc: cd: dd* = 8.3: 1.0: 9.5: 1.2: 22.6; or 15.2: 1.8: 17.5: 2.3: 41.6% (H). Ventral setal couples absent from XVIII; those of XVII and XIX modified as enlarged penial setae; genital setae not demonstrable. Nephropores not recognizable. Clitellum well-developed, saddle-shaped, extending over XIII-XIX, with a mid-ventral gap that extends to, or slightly lateral of, *ab* lines. Male pores not visible. Prostatic pores 2 pairs, in XVII and XIX, each pore on a strongly protuberant oval papilla which is equatorial in line with the ventral setal couples (*ab*) relative to adjacent segments; the papillae of a side linked by a clearly developed narrow seminal groove which is bent medially (not forming parentheses) and is transversely incised by intersegmental furrows 17/18 and 18/19 and an intrasegmental groove of XVIII; the entire male genital area wider than long and not depressed. Genital markings: a broad, unpaired midventral pad extending laterally well beyond *b* lines, intersegmental in 10/11 and 14/15 and 21/22 but extending almost to the setal arcs of each adjacent segment; each pad traversed by a groove corre-

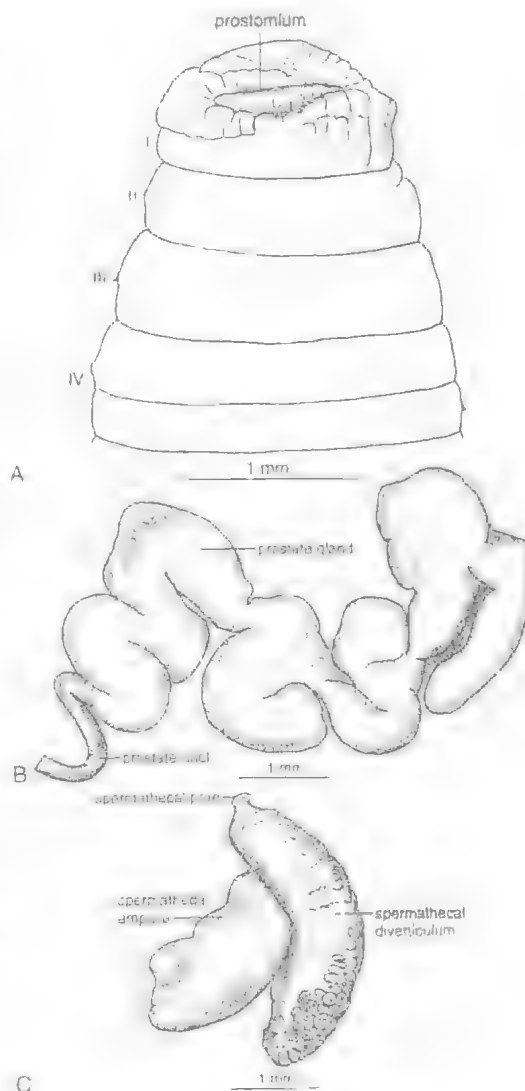


FIG. 18. *Neodiplotrema mcdonaldi* sp. nov. Holotype, QMG212005. A, dorsal view in region of prostomium. B, right prostate of XVII, with penial setae omitted. C, right spermatheca of IX.

sponding with the intersegmental furrow. Further markings a suggestion of a small papillae posteromedian to the prostatic porophores of XVII. Genital tumescences absent. Female pores, with elliptical borders, a pair near the anterior margin of XIV, in *ab*. Spermathecal pores 2 pairs, in 7/8 and 8/9, in or slightly lateral of setae *b*; each on a conspicuous elliptical papilla which is wider than a setal couple.

Septa 6/7-9/10 strongly thickened. Dorsal blood vessel single, continuous onto the pharynx.

Last hearts in XIII; those in XI-XIII large, with conspicuous supraoesophageal and smaller dorsal connectives; those in X slender, though still apparently laterooesophageal; in IX anteriorly slender, with dorsal connective only. Gizzard moderately large and firmly muscular, in V, widening anteriorly. Oesophagus with a pair of lateral blood red dilations, with many closely situated circumferential vascular striae which correspond with low internal lamellae, in each of 1/2XII-XV; not pinched off from the oesophagus but true, sessile, calciferous glands as indicated by white granular contents which effervesce vigorously in dilute acid whereas the contents of the adjacent oesophagus and the intestine do not (H). Intestine commencing in XVII; a very deep bilaminar typhlosole commencing in XX (P5). No anterior tufted nephridia present. At least four micromeronephridia on each side in the intestinal region; no funnels seen. Caudally with three or four meronephridia on each side, of which at least the median one has a preseptal funnel. Holandric; large seminal funnels with spermatozoal iridescence in X and XI. Large racemose seminal vesicles a pair in each of XI and XII, each vesicle a compact mass, with a single connection to the anterior septum of its segment, divided into many small iridescent loculi. Dendritic ovaries with many egg strings in XIV. Prostate glands flattened very tortuous wide tubes investing the intestine, a pair in each of XVII and XIX; with a narrow S-shaped duct the ental fourth of which is transitional to the structure of the gland. Penisetal follicles immensely long and conspicuous, the posterior pair extending posterolaterally to join the body wall in XXIV. Penial setae exceedingly thin and filiform; a long ectal region ornamented with many long slender sinuous scales directed obliquely towards the tip and standing well up from the surface; each scale itself consisting of three or more parallel pointed strands; length of a well developed right posterior penial seta (straightened) = 6.7 mm. Genital setae not demonstrable. Spermathecae two pairs, in VIII and IX, the diverticulum (so identified by presence of sperm chambers) a tongue-shaped mass so large as to be visible on opening the specimen dorsally, resembling a seminal vesicle, its outer and terminal aspect with numerous small protuberant

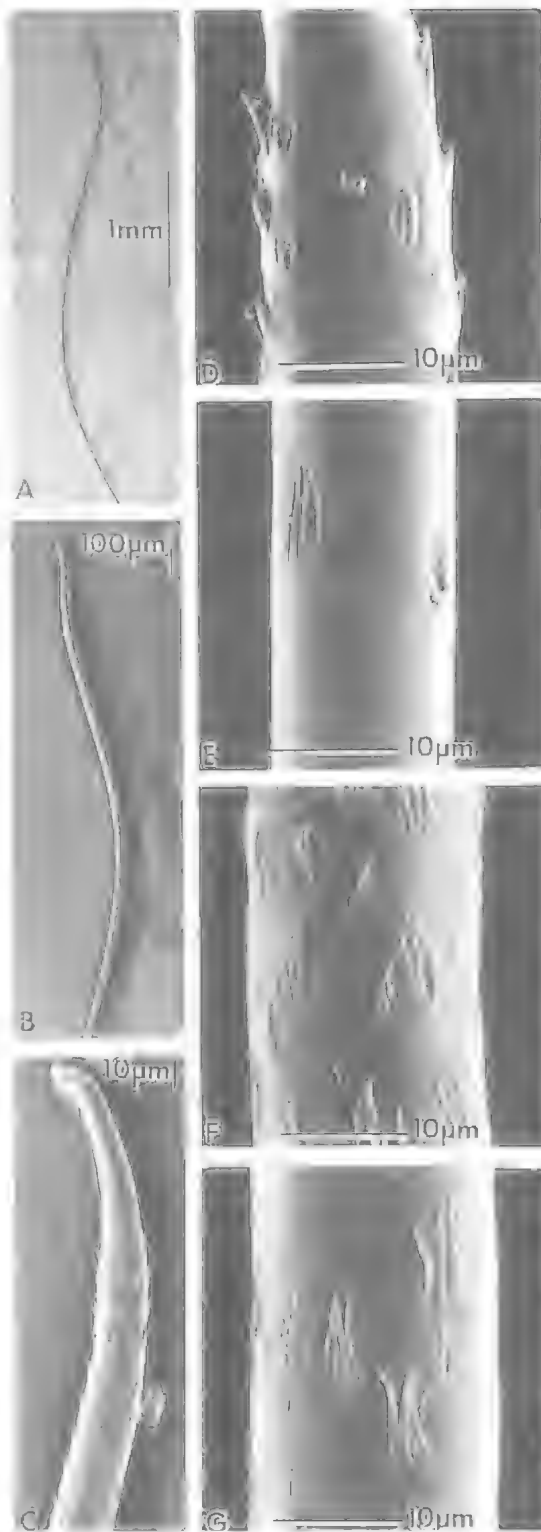


FIG. 19. *Neodiplotrema mcdonaldi* sp. nov. Holotype, QMG212005. Scanning electron micrographs of a right penial seta of XIX. A, seta, excepting base. B, higher magnification. C-G, appearance of seta from the tip to near the base.

chambers containing sperm balls; the ampulla a slightly smaller pointed sac appearing to be an appendage of the diverticulum; the duct a short narrow ectal continuation from the diverticulum. Length right spermatheca of IX, from pore to tip of diverticulum = 3mm; ratio length spermatheca: length duct = 17:1; length ampulla = 2mm.

**ETYMOLOGY.** Named for Keith McDonald who first collected this species.

**REMARKS.** *Neodiploptrema mcdonaldi* is distinguished from all other species of the genus by the large mammillated spermathecal diverticulum which exceeds the length of the ampulla and by the sinuous hair-like penial setae. A similar type of spermatheca occurs in *Diploptrema ridei* and, though less similar, in *D. shandi*. Close relationship of *N. mcdonaldi* to *D. ridei*, from Cape York and Melville Island, deserves consideration in view of considerable similarities of their genital fields.

***Neodiploptrema paripunctata* sp. nov.**  
(Figs 20-23; 39)

**TYPE LOCALITY.** 14°33'27"S 144°38'08"E, Altanmoui Section, Cape Melville National Park, altitude 52010 m, in mesophyll vine forest, with feather palms, along creek, located from pig diggings, K. McDonald, P.J. Leithbridge, 7 & 10 Apr 1995.

**MATERIAL EXAMINED.** HOLOTYPE, QMG213360. PARATYPE, P1 QMG213361.

**DESCRIPTION.** Length 150mm. Width (mid-clitellar) 3.8mm. Segments 171 (H). Colour brown in ethanol with a pale grey-brown clitellum. Prostomium probolous. Peristomium with anterior parallel grooves; approximately as long as segment II; not bisected ventrally. First open dorsal pore 18/19, but occluded pores present on the remaining, more anterior, segments of the clitellum (H). Setae 8 per segment, in regular longitudinal rows throughout; ventral setal couples of XVIII present immediately median to the seminal ridges; those of XVII and XIX modified as enlarged penial setae; genital setae absent; in XII,  $aa: ab: bc: cd: dd = 3.6: 1.0: 4.2: 1.0: 18.0$ ; or  $10.6: 2.9: 12.4: 2.9: 52.9\%$  (H). Nephropores not visible. Clitellum saddle-shaped, protuberant, XIII-XIX; ventral margins well above *b* lines. Prostatic pores 2 pairs, in XVII and XIX, coincident with the protuberant penial setae, in line with the ventral setal couples (*ab*) of other segments; the pores on each side on small porophores which are not distinguished from a tumid parenthetic ridge which bears a simple seminal groove. A

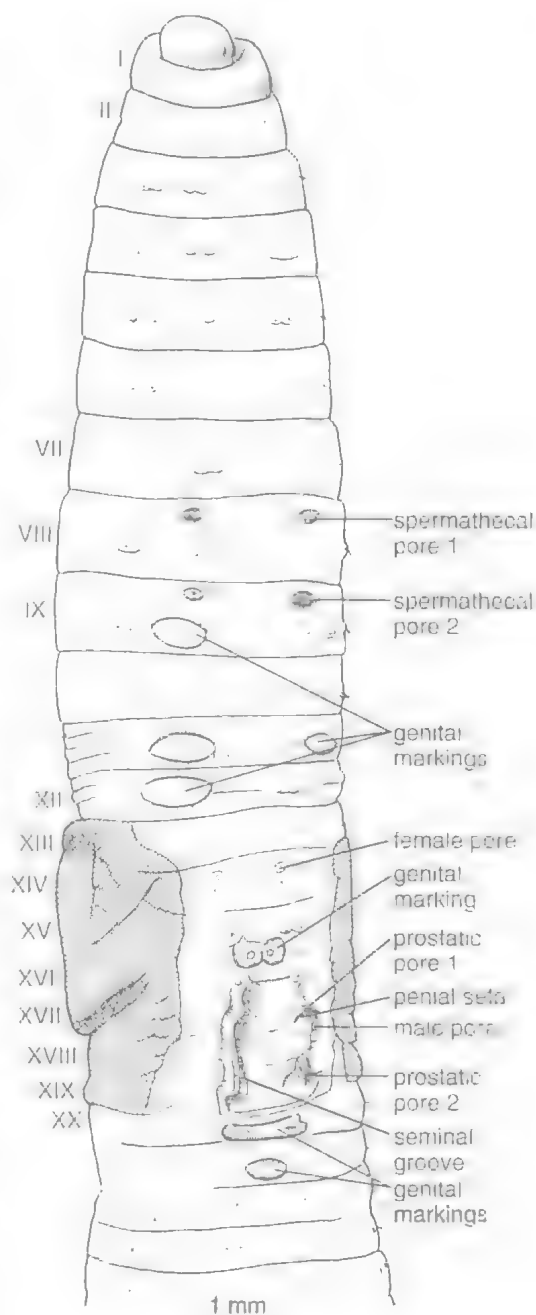


FIG. 20. *Neodiploptrema paripunctata* sp. nov. Holotype, QMG213360. Ventral view of forebody and clitellar region.

deep midventral depression present between the seminal grooves. Male pores a pair of minute orifices, on the seminal ridges, at the level of

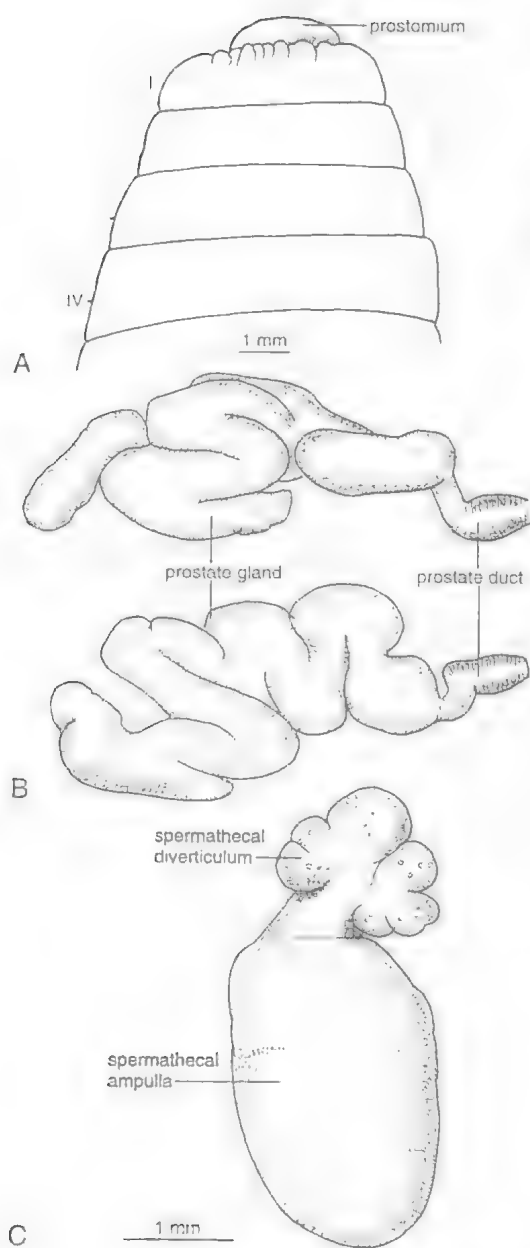


FIG. 21. *Neodiplotrema paripunctata* sp. nov. Holotype, QMG213360. A, dorsal view in region of prostomium. B, left prostates; penial setae omitted. C, right spermatheca of IX. B and C same scale.

17/18 and shortly lateral of *b* lines. Female pores in small oval fields anterior to the ventral setal couples (*ab*) of XIV. Spermathecal pores 2 pairs, a short distance posterior (relaxation artefact?) to 7/8 and 8/9, in *b* lines. Genital markings paired or

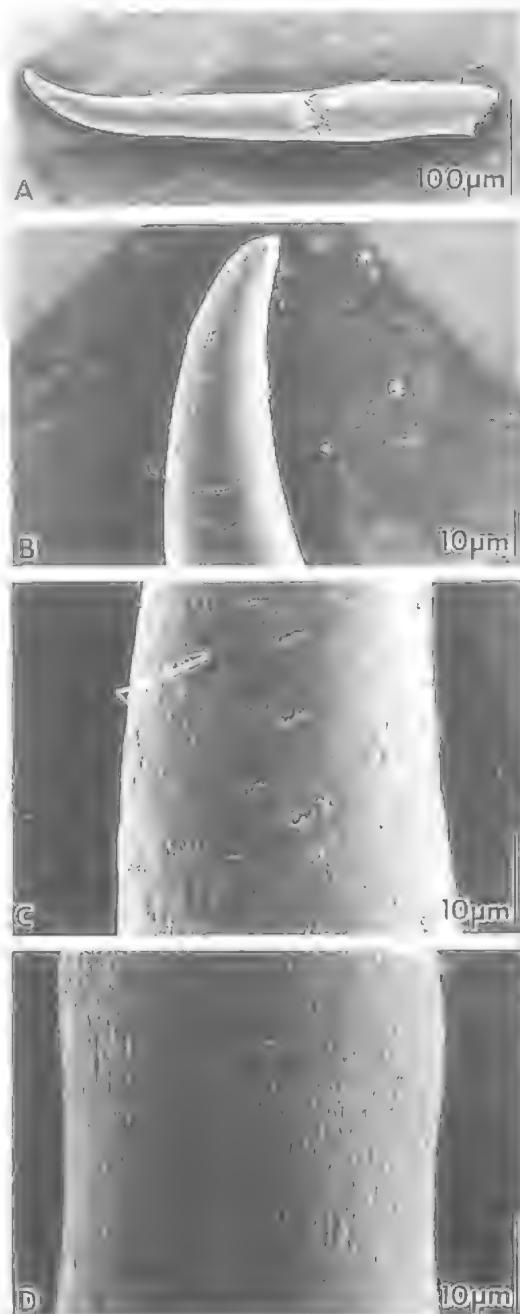


FIG. 22. *Neodiplotrema paripunctata* sp. nov. Holotype, QMG213360. Scanning electron micrographs of a ventral seta of VIII. A, seta, showing node typical of somatic setae. B-D, appearance of seta from the tip to near the base.

unilateral pale non-protuberant oval patches, bordered by brown pigment, lateral of or just including setae *b*, in IX, XI and XII (H, P1) and in X

(P1); a pair of medianly contiguous papillae mid-ventrally in 15/16 (H, P1); a midventral transverse postsetal pad in XX (H, P1); a small indistinct midventral oval pad in the posterior half of XXI (H).

Septa 7/8-11/12 fairly strongly thickened. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII; those in X-XIII latero-oesophageal, with supra-oesophageal connective larger than the dorsal connective; commissurals in IX, and anteriorly, slender and with dorsal connectives only. Gizzard very large, cylindrical, slightly widening anteriad, moderately firm and muscular, in VI(?), i.e., anterior to the diaphanous septum 6/7. Oesophagus lacking calciferous glands. Intestine commencing in XIX, not reaching full width until XXIV. A pair of moderate-sized, conical anterolateral diverticula on the intestine in XXVIII. No typhlosole found. Large tufted nephridia in II and IV send composite ducts to the wall of the buccal cavity and are accompanied laterally by many micromeronephridia; in the oesophageal region at least 12 micromeronephridia on each side, apparently all astomate and with no enlargement of the median pair; caudally with 8 meronephridia on each side, the medianmost one enlarged as a megameronephridium with a preseptal funnel; the lateral nephridia apparently lacking funnels (H). Holandric; iridescent seminal funnels in X and XI. Seminal vesicles in IX and XII; sacciform, those in IX subdivided into two or more portions, and accompanied by a row of small vesicles; those in XII each forming an exceptionally large lobulated sac. Ovaries not detectable. Two subequal pairs of thickly tubular very tortuous prostates in XVII and XIX, limited to their segments, their surfaces minutely mammillated; the ectal duct with a stout, muscular ectal region and a shorter less muscular region, bent relative to this, which is narrow at its origin from the gland. Vasa deferentia not traceable. Penisetae follicles overlying the prostate ducts. Penial setae curved in an arc, the tip strongly reflexed on itself or with a scroll-like expansion; ornamentation, on the shaft, consisting of weakly developed jagged transverse lines, each encircling less than one fourth of the circumference, and spaced longitudinally at approximately 10  $\mu$ m intervals or these jagged lines very few and scarcely visible; length of a well developed left penial seta of XVII = 2.5mm; greatest width approximately 35  $\mu$ m (H). Ventral setal couples of VIII and IX unmodified. Spermathecae two pairs, in VIII and IX; each with a large ovoid ampulla and a

short narrower but poorly demarcated duct which is hidden except for its ectal end by a rosette-shaped multiloculate diverticulum which is incised slightly or deeply into approximately 8 large loculi in which many minute iridescent sperm balls are visible. Length right spermatheca of IX = 8.2mm; length ampulla = 2.9; ratio of length spermatheca: length duct = 5.3; diameter of diverticulum 1.6mm (H).

ETYMOLOGY. *paripunctata*, referring to the paired anterior oval patches.

REMARKS. The pair of closely apposed genital markings in 15/16 is distinctive of *N. paripunctata*. This and the absence of large denticulations of the penial setae, is among features distinguishing *N. paripunctata* from the sympatric *N. altanmoui*. Intestinal diverticula are known in pheretimoids, in the Megascolecinae, but have not previously been observed in the Acanthodrilinae.

#### Kayarmacia gen. nov.

DIAGNOSIS. A pair of combined male and prostatic pores, associated with penial setae, on XVII. Spermathecal pores 1 pair, in intersegmental furrow 7/8. Gizzard in V. Oesophagus lacking calciferous glands. Holonephric; nephridia avesculate. Holandric. Prostate a single pair of tortuous tubes, each with an exceptionally long tortuous muscular duct which opens in common with the equally thick and muscular ectal end of the vas deferens (ejaculatory duct). Spermathecae a pair in VIII; diverticulum, with nacreous sperm masses.

DESCRIPTION. Small worms, less than 75mm long. Dorsal pores (always?) present. Setae 8 per segment, closely paired; the lateral couple (*cd*) narrower than the ventral couple (*ab*). Clitellum anterior to the male pores; annular. A pair of combined male and prostatic pores, associated with penial setae, on XVII. Genital markings present in the vicinity of the male pores. Genital tumescence and modified ventral setae present or absent in the spermathecal region. Female pores presetal in XIV. Spermathecal pores 1 pair, in intersegmental furrow 7/8.

Dorsal blood vessel single. Last hearts in XIII, those in X-XIII large, heart-like and latero-oesophageal, the connective to the supra-oesophageal vessel larger than that to the dorsal vessel; commissurals in IX anteriorly slender, with dorsal connective only. Gizzard large,

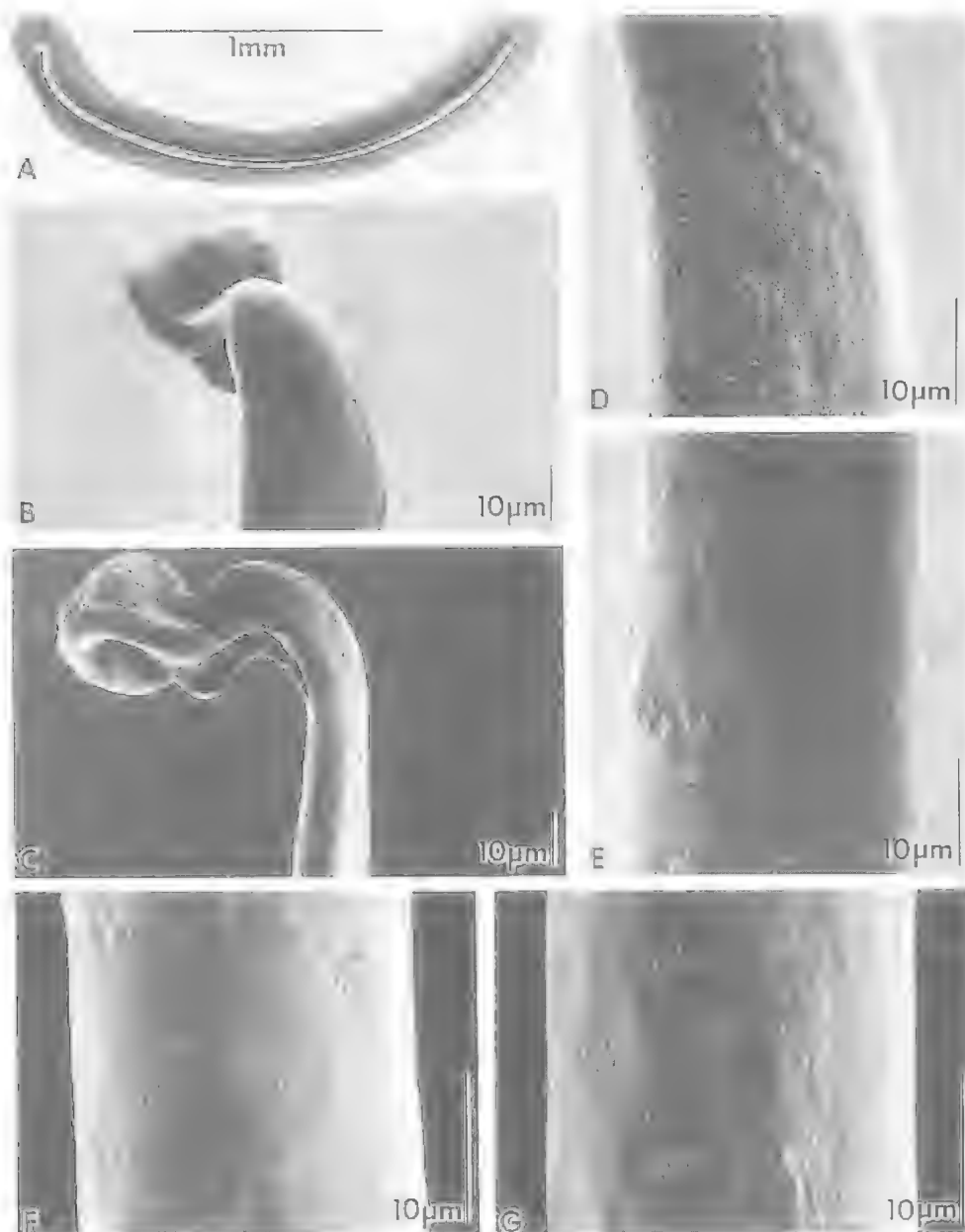


FIG. 23. *Neodiplotrema paripunctata* sp. nov. Holotype, QMG213360. Scanning electron micrographs of a left penial seta of XVII. A, seta. B-E, appearance of seta from the tip to near the base. F and G, ornamentation of the posterior regions of a left penial seta of XIX.

strongly muscular in V. Oesophagus lacking cal-ciferous glands. Intestine commencing in XVII. Holonephric; avesciculate ducts apparently discharging in mid *bc* or *c* lines; true anterior tufting not developed. Holandric. Racemose seminal vesicles in IX and XII. Ovaries in XIII. Prostate glands extending through several segments; a

single pair of tortuous tubes, each with an excep-tionally long tortuous muscular duct which winds forwards to open at the male pore in common with the equally thick and muscular ectal end of the vas deferens (ejaculatory duct). Spermathecae a pair in VIII, opening at the anterior border; diver-ticulum, with nacreous sperm masses.

**ETYMOLOGY.** *Kayarmacia*, based on the name of the collector, K.R. McDonald. Gender masculine.

**TYPE SPECIES.** *Kayarmacia adelphicus* sp. nov.

**OTHER SPECIES.** *Kayarmacia queenslandicus* (Michaelsen, 1916).

**DISTRIBUTION.** Cape York Peninsula.

**REMARKS.** *K. adelphicus* is chosen as the type species for *Kayarmacia* as identification of *K. queenslandicus* with Michaelsen's species, though made with confidence, is subjective and later changes to its synonymy, though unlikely, would cause confusion if were selected as the type species.

Michaelsen (1916) placed the Alice River specimens in *Rhododrilus*, features of this genus being of location of male pores in segment XVII, presence of a gizzard, and absence of nephridial bladders. However, these are insufficient reasons for considering *R. queenslandicus* to be congeneric with the New Zealand type species of the genus, *Rhododrilus minutus* Beddard 1889, as the latter species has four pairs of spermathecal pores and, more significantly, has the male and prostatic pores located separately on XVII. The mere presence of male and prostatic pores on XVII whether combined or separate is not unique to one genus, as it is seen *inter alia* in the acanthodriline genus *Microscolex* and is the typical condition in the Oecnerodrilinae and Eudrilidae. Nevertheless, it is likely that location on XVII represents a microscolecine reduction from an acanthodrilin arrangement of male pores (male pores on XVIII, prostatic pores on XVII and XIX) and that *Kayarmacia* is referable to the subfamily Acanthodrilinae and not to the Megascoclecinae.

The thickening of the distal ends of the vasa deferentia and their opening in common with the unusually long prostate ducts distinguishes *Kayarmacia* from other megascoclecine genera. Inclusion in the Oecnerodrilidae, a family in which male and prostate ducts may be swollen, is precluded by several features, including the non-oecnerodriline condition of the oesophagus. Native Oecnerodrilidae are unknown from Australia.

*Rhododrilus glandifera* Jamieson, 1995, is excluded from *Kayarmacia* by location of the spermathecal pores in intersegmental furrow 8/9, not 7/8, and, more significantly, the absence of thickening of the vasa deferentia, and the minute size of the apparently separate prostate ducts. That *R. glandifera* is congeneric with *Rhododrilus* is, nevertheless, doubtful and placement in that

genus must be regarded only as provisional. It may well have closer affinities with *Diplocrema* than does *Kayarmacia*.

***Kayarmacia adelphicus* sp. nov.**  
(Figs 24-27; 39)

**TYPE LOCALITY.** (1) 14°16'54"S 144°27'30"E, Cape Melville National Park, along creek bank, closed canopy, altitude ca. 100m, K.R. McDonald, L.A. Jackson, 24 Feb 1995. (2) Same, 14°16'54"S 144°27'30"E, 18 Feb 1995.

**MATERIAL EXAMINED.** HOLOTYPE. (1) QMG-213378 ex 211497 (part) (includes microscope slide of male ducts). PARATYPES. (1) P1-5 QMG211497 (with several not designated types); (2) P6 & 7 QMG211495.

**DESCRIPTION.** Length 25-39mm, 28mm (H). Width (midclitellar) 1.8-(H)2.6mm. Segments 102 (H). Pigmentless greyish buff in ethanol. Prostomium proepilobous (H) or epilobous 1/2. Peristomium approximately as long as segment II. Dorsal pores sporadically visible from shortly anterior to the clitellum (verified by exudation of alcohol when specimen is placed in water). Setae closely paired; in XII, *aa: ab: bc: cd: dd* = 8.2: 1.0: 7.7: 0.9: 18.1; or 18.1: 2.2: 16.9: 1.9: 40.0%. Clitellum in XIII-anterior XVII; annular but ventrally interrupted from the anterior third of XVI posteriorly, to about mid *bc* by the male field; setae and intersegmental furrows present on it. A pair of large, globose but anteriorly pointed strongly protuberant papillae each bearing the combined male and prostatic pore on XVII; in *ab*; the walls of the papillae diaphanous and revealing internally the large penial setae which support its anterior protrusion (H), or the penial setae strongly protuberant (P1, 2). Genital markings a pair of indistinct swellings, at setae *ab* of XVI and XVIII; a midventral elliptical papillae postsetally in XVIII or (P6) in XVI. Genital tumescence and modified ventral setae developed on the right side in VII (H) or paired in IX (P1, 2). Female pores minute, immediately anterior to setae *a* of XIV. Spermathecal pores 1 pair, in intersegmental furrow 7/8, shortly lateral of *b*; each a lateral slit in an oval papilla.

Septa 8/9 and 9/10 the thickest, moderately strongly thickened, Dorsal blood vessel single. Last hearts in XIII, those in X-XIII large, heart-like and latero-oesophageal, the connective to the supraoesophageal vessel larger than that to the dorsal vessel; commissurals in IX anteriorly slender, with dorsal connective only. Gizzard very large, strongly muscular but compressible, ellip-

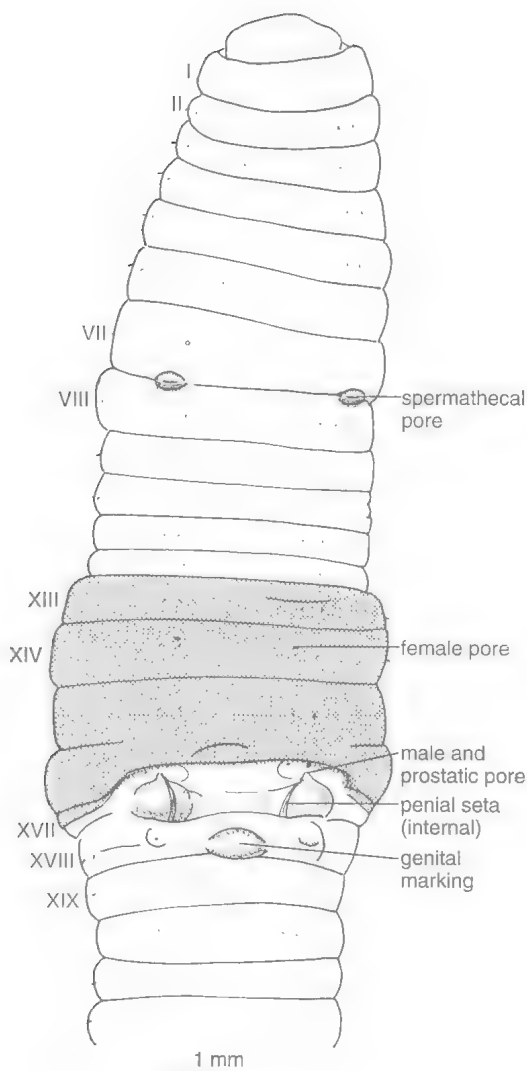


FIG. 24. *Kayarmacia adelphicus* gen. et sp. nov. Cape Melville National Park, holotype, QMG213378. Ventral view of forebody and clitellar region.

soidal though widening anteriorly, in V. Oesophagus lacking calciferous glands. Intestine commencing, with abrupt expansion, in XVII (H, P2). Holonephric; nephridial bodies commencing in II; avesiculate ducts apparently discharging in mid *bc*; anterior tufting not developed. Holandric; iridescent sperm funnels in X and XI. Large, several lobed racemose seminal vesicles in IX and XII (H, P2). Small ovaries, with few oocytes, in XIII. Prostate glands visible externally through the body wall in the holotype extending from XVII to XXVIII; a single pair of tortuous tubes, each with an exceptionally long tortuous muscu-

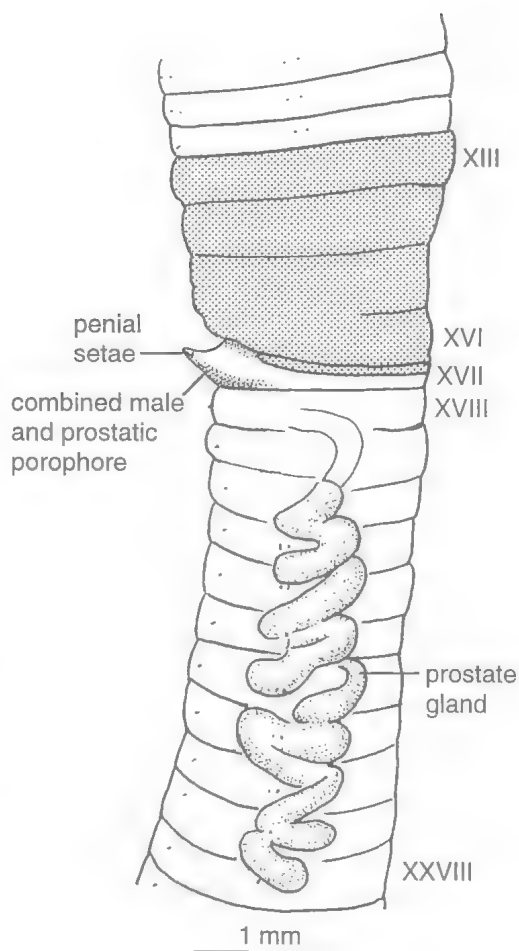


FIG. 25. *Kayarmacia adelphicus* gen. et sp. nov. Cape Melville National Park, holotype, QMG213378. Lateral view of male genital region, showing prostate gland seen through body wall.

lar duct which winds forwards to open at the male pore in common with the equally thick and muscular ectal end of the vas deferens (ejaculatory duct) (H, P2); the prostate duct and ejaculatory duct pass separately but in contact to the tip of the male porophore (confirmed in cleared mount). Penial setae, only 1 on each side; stout, ectally curved to form a hook; length 1.2mm, greatest, basal, width ca. 70µm; ornamentation consists of droplet-like or many wart-like elliptical prominences on the 'dorsal' and 'ventral' surfaces of the curvature, the sides of the latter being smooth; on the ventral surface, however, the prominences are reduced to minute scattered but densely situated points or cicatrices. Genital setae present on right



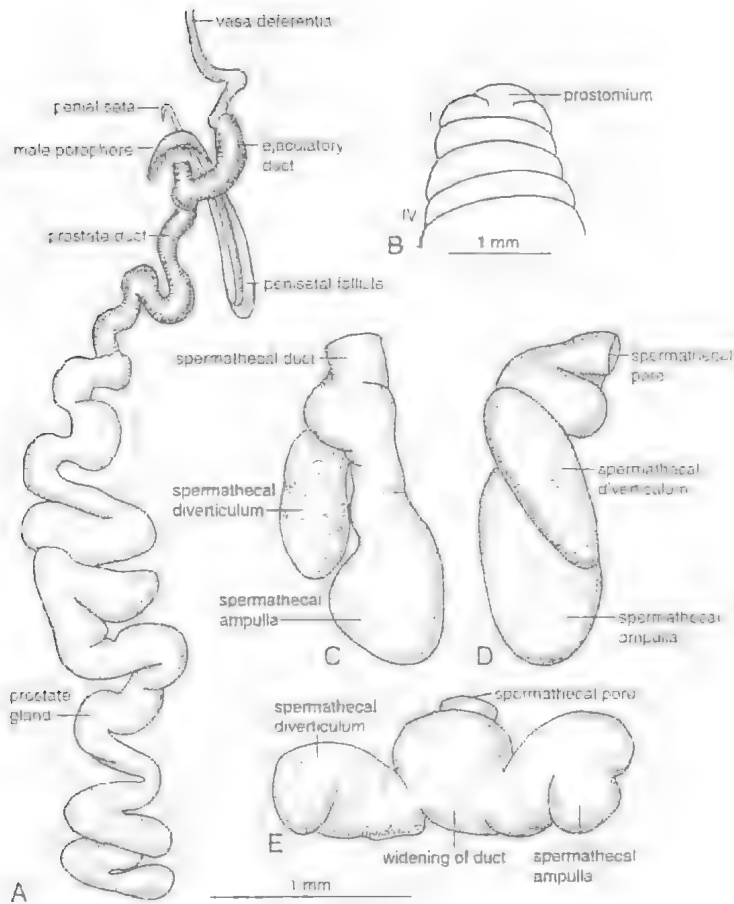


FIG. 26. *Kayarmacia adelphicus* gen. et sp. nov. Cape Melville National Park, holotype, QMG213378. A, left prostate and male duct, with penisal follicle. B, dorsal view in region of prostomium. C and D, two views of left spermatheca. E, Paratype 2, QM G211497, left spermatheca. A, C-E same scale.

in VII (H) or bilateral in VIII (P2); length of left genital seta of VIII, 0.76mm; shaft gently curved but a short basal region strongly curved; tip pointed, very slightly expanded beneath the point; ornamentation four (?) longitudinal series, each of about five large gouges or notches. Spermathecae a pair in VIII, opening at the anterior border; each with a large ovoid ampulla; the duct of which consists of three regions in longitudinal succession: an ental third which is approximately tubular and is well demarcated from the ampulla, a swollen intermediate region which receives the diverticulum, and an ectal third which forms a wide, short, muscular, tubular duct. Diverticulum elongate ellipsoid, filled with nacreous sperm masses but uniloculate, with a narrow connection to the spermathecal duct. Length left spermatheca

= 1.7mm; length ampulla = 0.88mm; ratio length spermatheca: length duct = 2.1; length diverticulum = 1.0mm (H). In P2, the swollen part of the duct is approximately as large as the ampulla.

**ETYMOLOGY.** *adelphicus*, from the Greek Adelphos, brother, referring to its putative adelpho-group relationship to *K. queenslandicus*.

**REMARKS.** *Kayarmacia adelphicus* is morphologically very close to the prior *K. queenslandicus* (q.v.) but geographical separation by the Great Dividing Range suggests that the presence in it of genital setae, whereas these appear always to be absent from *K. queenslandicus*, indicates vicariation of the two taxa from a common ancestor. Strong support for recognizing the two as separate species is seen in the very different ornamentation of the penial setae. It consists of scattered droplet-like prominences in *K. adelphicus* contrasting with tooth rows which 'ventrally' are united in extensive transverse rows in *K. queenslandicus*. The distinctive structure of the male and prostatic ducts seen in both species is here regarded as a generic character. The genital

setae, with longitudinal series of large gouges or notches, are of the type seen also in *Diploptrema* and the New Caledonian genus *Acanthodrilus* and indicate relationship with these genera.

This species was found in humic sandy soil under closed canopy on a creek bank near the edge of the Cape Melville Altanmoui granite boulder fields.

***Kayarmacia queenslandicus* (Michaelsen, 1916). New combination (Figs 28-30; 39)**

*Rhododrilus queenslandicus* Michaelsen, 1916: 4-6, Pl. 1, fig. 9-11.

**MATERIAL EXAMINED.** SYNTYPES. ca. 15°S., Cape York, banks of Alice River, a single much dis-

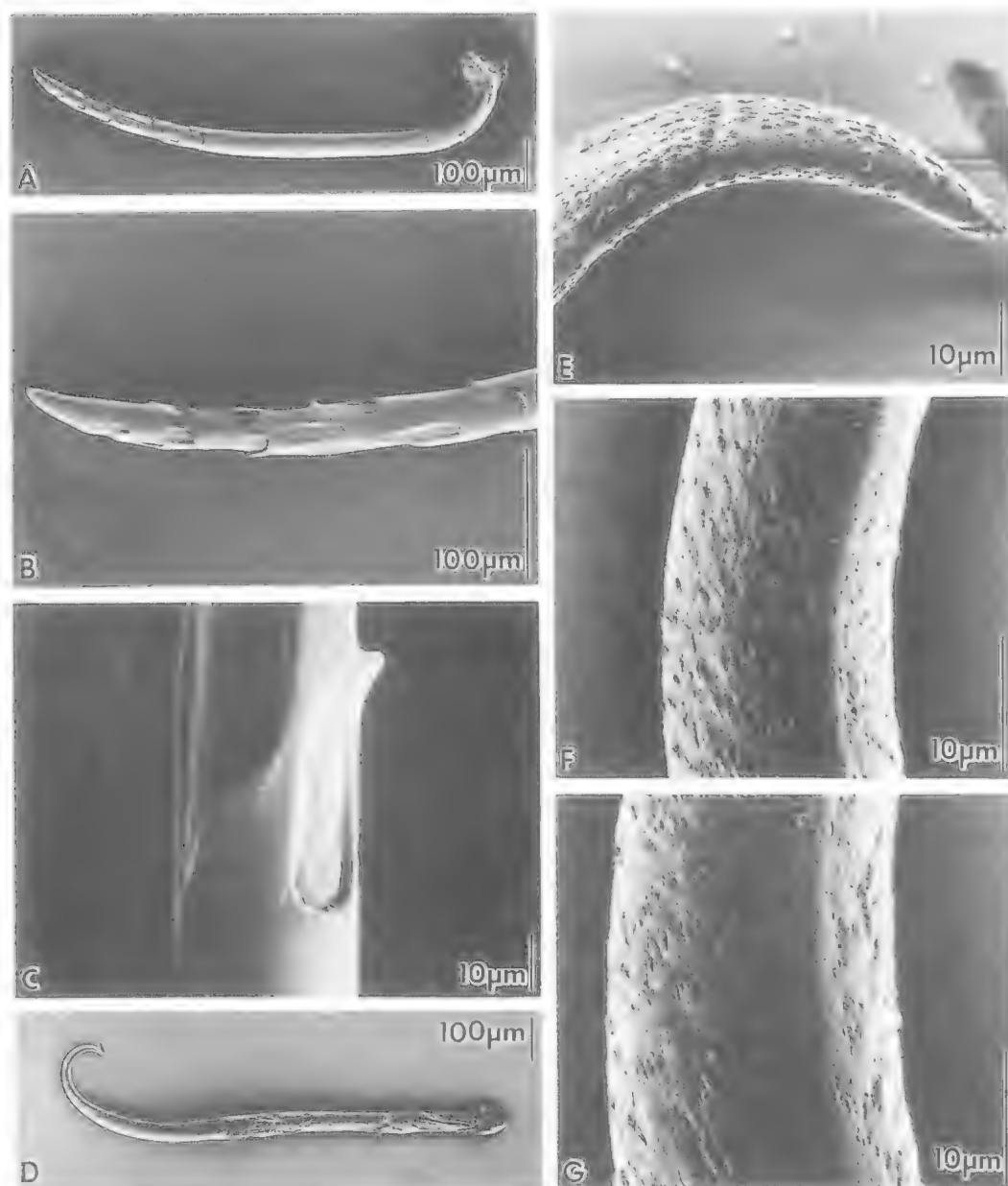


FIG. 27. *Kayarmacia adelphicus* gen. et sp. nov. Cape Melville National Park. A, paratype 2, QMG211497, left genital seta of VIII. B and C, tip and shaft of same. D, Holotype, QMG213378, right penial seta. E-G, appearance of seta shown in D from the tip to near the base.

sected specimen labelled 'Kap York, Mjöberg, Alice River, Hamburg Museum V8487. NEW MATERIAL. 15°27'45"S 142°10'12"E, Emu Lagoon, Alice-Mitchell Rivers National Park, altitude 222m, top-soil on sandy levee bank, open woodland, K.R. McDonald, 9 Feb 1993. ex QMAcc#2344, specimens 1-6 QMG213385.

**DESCRIPTION.** Length 49-75mm. Width (mid-clitellar) 1.2-1.9mm; greatest width (forebody) 2.3mm. Segments 124-143 (shortest and longest specimens, S3 and 5). Pigmentless in ethanol; clitellum greyish buff. Prostomium epilobous, ca. 1/4; small, broad and open. Peristomium approximately as long as segment II. Dorsal pores spo-

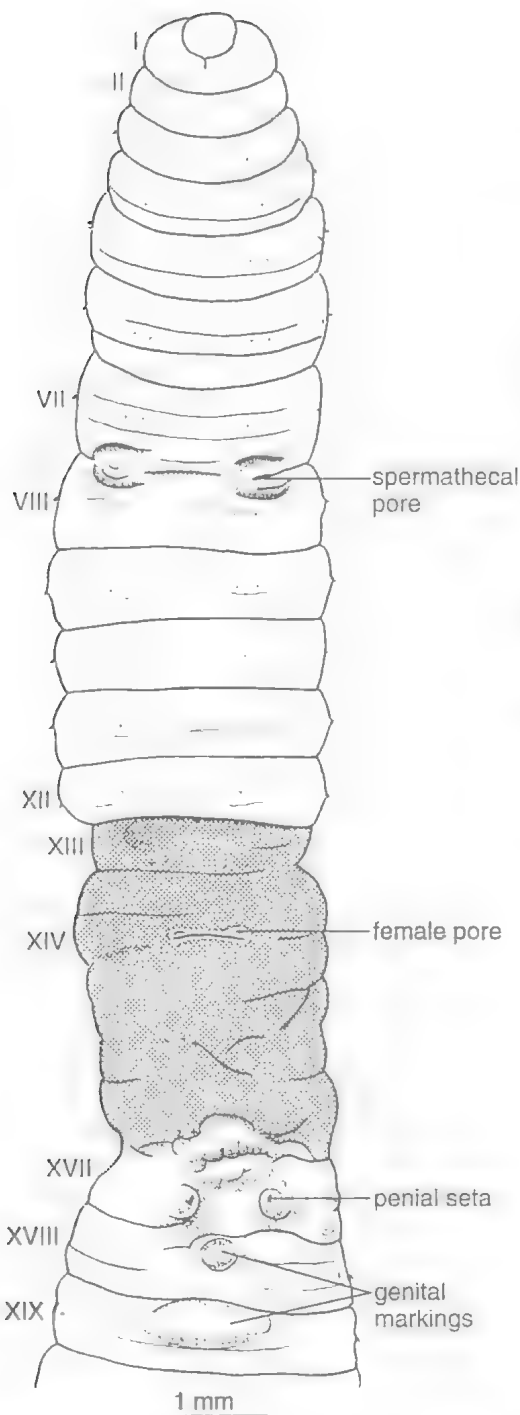


FIG. 28. *Kayarmacia queenslandicus* (Michaelsen, 1916). Emu Lagoon, Alice-Mitchell Rivers National Park, specimen QM Acc#2344, QMG213385. Ventral view of forebody and clitellar region.

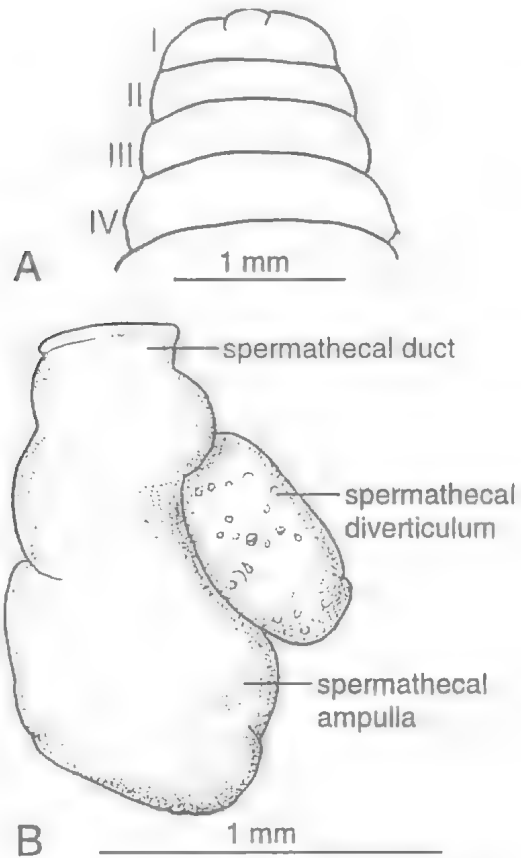


FIG. 29. *Kayarmacia queenslandicus* (Michaelsen, 1916). Emu Lagoon, Alice-Mitchell Rivers National Park, specimen QM Acc#2344, QMG213385. A, dorsal view in region of prostomium. B, right spermatheca.

radically visible from shortly anterior to the clitellum (verified by exudation of alcohol when specimen is placed in water). Setae closely paired; in XII,  $aa: ab: bc: cd: dd = 6.6: 1.0: 6.1: 0.7: 26.1$ ; or  $13.6: 2.1: 12.5: 1.5: 54.2$ . Clitellum annular, XIII-XVI; setae normally developed. Male genital field: a deep transversely elliptical depression in XVII, preceded posteriorly in XVI by a midventral, transverse glandular elevation, and extending somewhat onto XVIII median to a pair of strongly protuberant combined male and prostatic porophores, the median borders of which project ventromedially over the depression, the lateral borders of which are poorly distinguished from the lateral region of the segment; from the summit of each papilla, in setal line *a*, projects a penial seta; etc. An indistinct hemispheroidal midventral genital markings

present presetally in XVIII; a larger indefinite tumescence presetally in XIX (S1), or a hemispheroidal midventral genital marking present post-setally in XVIII. Female pores a pair of deep punctuations very shortly anterior median to seta *a* of XIV. Spermathecal pores 1 pair, in intersegmental furrow 7/8, in or shortly lateral of *b*; each with a large approximately ellipsoidal epidermal elevation surrounding it which extends well laterally of *b* and to or median of *a* and is bounded anteriorly by a crescentic groove.

Septa 5/6 (S2), 6/7 (S1)-8/9 the strongest, moderately strongly thickened. Dorsal blood vessel single, continuous on to the pharynx. Last hearts in XIII; those in X-XIII large and heart-like with large connective to the supraoesophageal vessel and slender connective to the dorsal vessel; those in IX anteriorly slender, with dorsal connective only. Gizzard large, strong, glossy, muscular though compressible. Oesophagus lacking calciferous glands; segmentally slightly swollen and vascularized in VIII-XVI, especially vascular in X-XIV (S1) or XI-XVI (S2). Intestine commencing in XVII but not sharply demarcated from the oesophagus (S1, 2). Typhlosole absent. Holonephric. Nephridia of II, III and especially IV enlarged and much lobed though not truly tufted; connection to the gut not detected (S2). Other nephridia with avascular ducts discharging anterior to the lateral setal couples, specifically in *c* (S1). Large male funnels in X and XI (S1, 2), with spermatozoal iridescence in S1. Seminal vesicles in IX and XII, racemose, much divided, those in XII the larger (S1); in IX only (immature) in S2. Paddle-shaped ovaries in XIII. Prostates tubular, extending from XVII to XXIV (S1, 2); zigzagged in S1, almost straight and very slender owing to immaturity in S2; at maturity (S1) the duct extending from XVII- 1/2XIX, with an abrupt bend in XIX; the short portion ental to the bend not noticeably muscular, the remaining, more ectal portion forming a wide, muscular, glossy tube extending forwards to the male porophore; vasa deferentia in XVI and XVII forming a muscular tube of similar appearance but slightly wider (ejaculatory duct), a short region ental to this, also in XVI, is more slender and represents the posterior portion of the unmodified more anterior region of the conjoined vasa deferentia. Penial seta ca. 0.96mm long; only one on each side; the tip curved in a hook as in *K. adelphicus* (S2), extending from XVII into anterior XIX (S1, 2); the curved apical portion ornamented 'dorsally' and 'ventrally' by extensive finely toothed transverse rows but the sides

smooth; the ventral tooth rows linked up transversely so as to straddle much or the whole of the ventral surface. Spermathecae a pair in VIII, opening at the anterior border, not fully mature in S2; in S1 each with a large ovoid ampulla; the duct of which consists of three regions in longitudinal succession: an ental third which is approximately tubular and is well demarcated from the ampulla, a swollen intermediate region which receives the diverticulum, and an ectal third which forms a wide, short, muscular, tubular duct. Diverticulum elongate ellipsoid, with numerous nacreous sperm masses which possibly represent non-protruberant sperm chambers, and with a narrow connection to the spermathecal duct. Length left spermatheca = 1.5mm; length ampulla = 0.9mm; ratio length spermatheca: length duct = 2.5; length diverticulum = 0.7mm.

**REMARKS.** The type locality is the Alice River, which Michaelsen (1916) wrongly thought to be a tributary of the Coleman River. Michaelsen's material was collected from the banks of the river but he recognized its at least potentially 'limnische Lebensweise'. The stated absence of dorsal pores would correlate with an amphibious existence. The water table is at the surface and in the rainy season most of the area, excepting the levee banks, is covered by water (K. R. McDonald, pers. comm.). However, in the new material dorsal pores are sporadically demonstrable though possibly vestigial.

Identification of the new material as *Rhododrilus* (now *Kayarmacia*) *queenlandicus* is based on close morphological similarity and collection near the type locality. The identification appears to be confirmed by the unusual ornamentation of the penial setae in which transverse rows of scales are present dorsally and ventrally on the apical curvature but the sides are smooth. The above account is derived solely from the new material. Michaelsen's description of *Rhododrilus queenlandicus* accords closely but some points of disagreement require mention. The clitellum is said to occupy XIII-XVII, in XIII and posterior XVII being less well developed, whereas in the Emu Lagoon specimens it ends with segment XVI. No accessory genital markings were present. The thickened end of the male duct was shown to open into the prostate duct whereas in the Emu Lagoon material these two ducts were shown to be closely apposed at the male pore but actual fusion has not been demonstrated. Two penial setae were seen in each follicle whereas one only is present on each side in

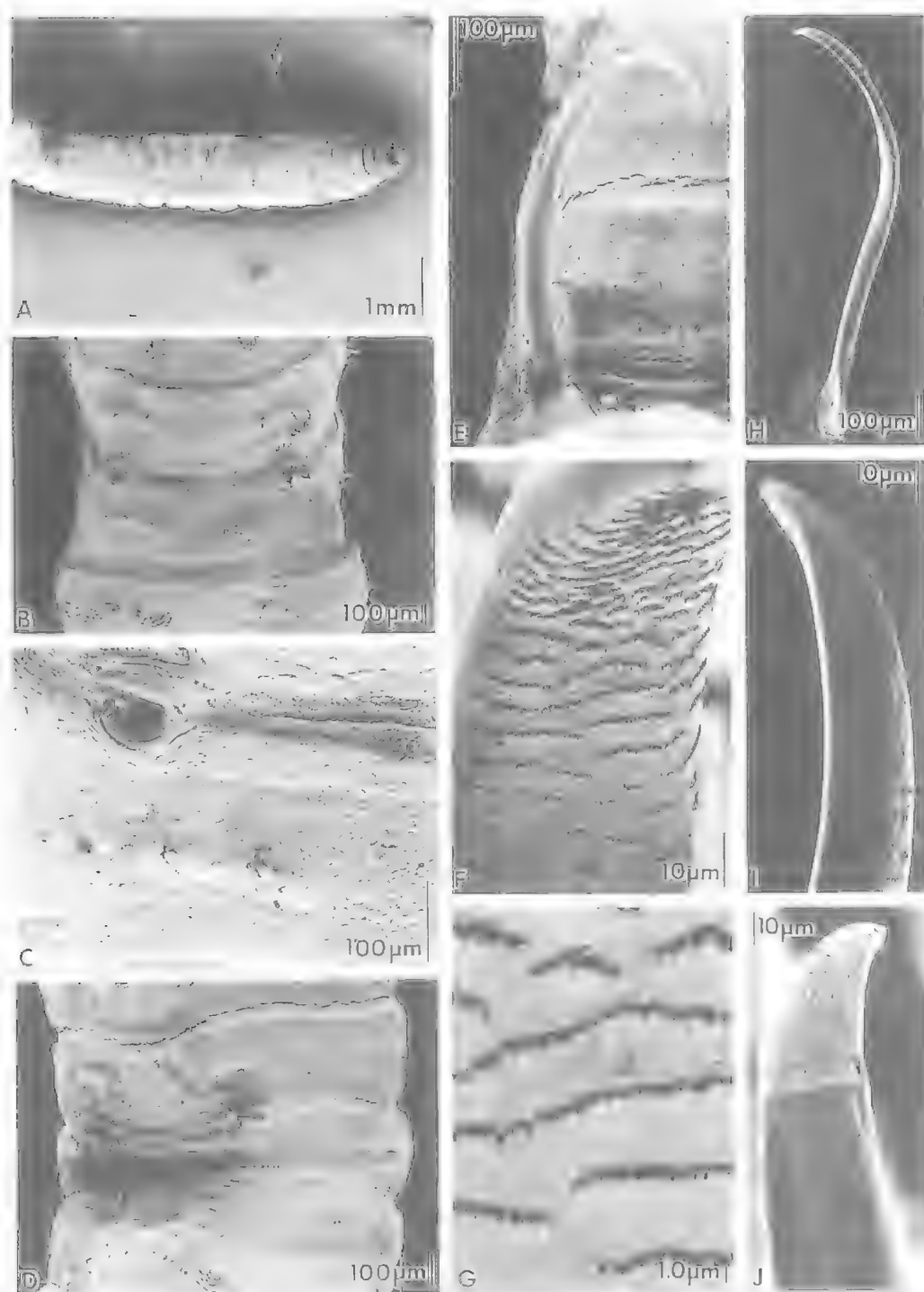


FIG. 30. *Kayarmacia queenlandicus* (Michaelsen, 1916). Emu Lagoon, Alice-Mitchell Rivers National Park, specimen QM Acc#2344, QMG213385. Scanning electron micrographs of specimen 6, QMG213385. A, ventral view. B, region of spermathecal pores. C, a right spermathecal pore. D, penial setae *in situ*. E, right penial seta *in situ*. F, ventral ornamentation of penial seta. G, same, higher magnification. H, penial seta of specimen 2. I, dorsal ornamentation of a penial seta of same. J, dorsal ornamentation of a penial seta of specimen 6.

the new material. Although the description of the spermathecae given by Michaelsen differs in some regards relative to that given here for the Emu Lagoon material, the differences are doubtfully significant and his illustration agrees well with that for the latter; the very wide duct illustrated for the type corresponds with the wide middle region of the duct in the new material. In view of the close similarities of the new material with the types, including the ventral ornamentation and smooth sides of the setal curvature, these differences of description do not appear to merit specific separation.

The close similarity of the material here identified as Michaelsen's *Rhododrilus queenslandicus* and the new species *Kayarmacia adelphicus* is discussed in the account of the latter. The specimen of *K. queenslandicus* in which the genital marking in XVIII is postsetal, as in *K. adelphicus*, further narrows the gap between the two taxa. If genital setae were found in *K. queenslandicus* retention of *adelphicus* as a distinct species would still be supported by the difference in ornamentation of the penial setae.

Subfamily MEGASCOLECINAE  
Genus *Terrisswalkerius* Jamieson, 1995

*Terrisswalkerius carbinensis* sp. nov.  
(Figs 31 & 32; 39)

TYPE LOCALITY. 16°30'30"S 145°16'30"E., Mt Carbine Tableland, 980m, Notophyll vine forest on granite, K.R. McDonald and C. Hoskins, 22 Jan 1996.

MATERIAL EXAMINED. HOLOTYPE. QMG212025. PARATYPES. P1, 3-9, QMG213392-213399; P2 QMG212026; P10 QMG213400.

DESCRIPTION. Length 25-51mm; H 46mm. Width 2- (H) 3mm. Segments 69-145; H 147. Pigmentless buff in ethanol, clitellum pale brown. Prostomium broad and probolous but the peristomium describing a wide V posterior to it. Dorsal canalicula absent. Peristomium slightly shorter than segment II; not bifid ventrally. First dorsal pore 4/5. Setae 49 in XII; 54 caudally (12 segments from posterior end); *aa*: *ab*: *bc*: *cd*: *yz*: *zz* = 2.1: 1.0: 0.8: 0.6: 0.6: 0.8; thus ventral break (*aa*) pronounced; dorsal break (*zz*), except anteriorly, hardly perceptible; all lines approximately straight. Nephropores clearly visible on the clitellum in a straight lateral series, in setal lines 12, anteriorly in their segments. Clitellum annular, XIV-XVII; intersegmental furrows weakly represented; dorsal pores almost occluded; setae present, male pores minute, each with a narrow

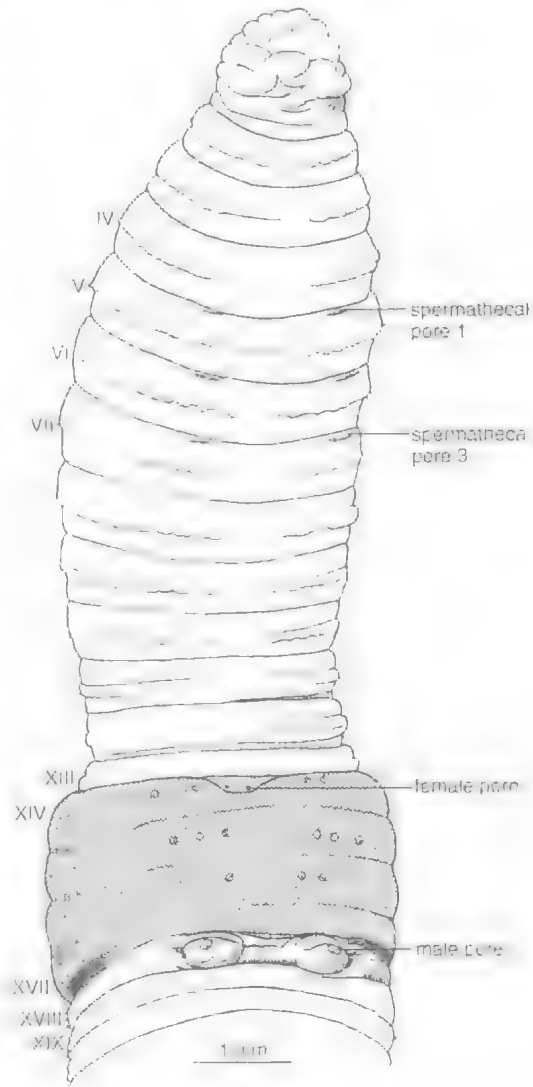


FIG. 31. *Terrisswalkerius carbinensis* sp. nov. Holotype, QMG212025. Ventral view of forebody and clitellar region.

pale border immediately lateral to setal line *b*, on a conspicuous oval papilla which extends from median to *a* to approximately *c* line; the papillae is an evaginated structure representing the termination of the unusually muscular prostate duct. Female pores a pair, presetally in *a* lines, in a pale field at the anterior border of the clitellum, in XIV. Spermathecal pores not visible but their sites indicated by a short transverse glandular ridge; approximately in *c* lines, immediately behind intersegmental furrows 4/5, 5/6 and 6/7.

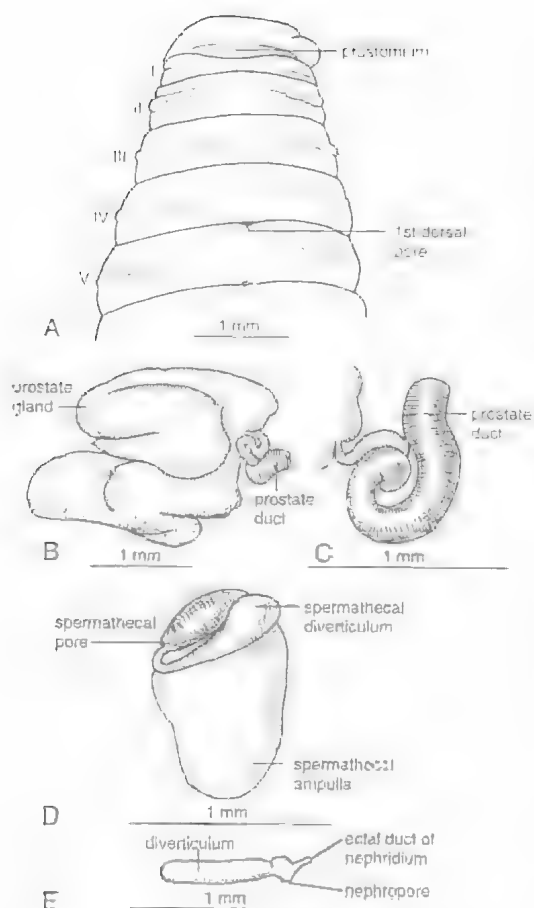


FIG. 32. *Terrisswalkerius carbinensis* sp. nov. Holotype, QMG212025. A, dorsal view in region of prostomium. B, left prostate. C, duct of same. D, right spermatheca of VII. E, left nephridium in anterior intestinal region.

Septa 7/8-12/13 strongly thickened. Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XII. Gizzard a very large, glossy, firmly muscular anteriorly slightly widening cylinder; anterior to septum 6/7; its posterior end at the level of segment IX; septum 5/6 attached to it near its anterior limit but apparently not investing it. Large pharyngeal glands in two or more preceding segments to not envelope the gizzard. Oesophagus greatly dilated and obliquely striated in XVI; the striations coinciding with numerous deep internal lamellae projecting into the lumen of what is here considered an unpaired calciferous gland. Intestine commencing in XIX in which it is constricted by the prostates. Nephridia simple stomate, vesiculate, holonephridia; the first blad-

ders anteriorly in II elongate pyriform, ad-iverticulate; anteriormost nephridia forming a thick coiled tube but not tufted; bladders in the intestinal region with a small expansion where the duct approaches the nephropore and large lateral digitiform portion constituting a diverticulum. Compacted sperm masses and well developed nacreous seminal funnels paired in each of X and XI; seminal vesicles a pair of large smooth sacs in IX and a pair of racemose, deeply dissected masses in XII; no pseudovesicles in XIII. Large laminar ovaries with many strings of large oocytes, and compact oviducal funnels, in XIII; ovisacs absent. Prostates large, tubuloracemose, with very thick adpressed sections in a zigzagged configuration which are closely adpressed so as to give the entire gland a racemose appearance; both embracing the oesophagus and intestine at their juncture and meeting dorsally above the gut; each with a long much coiled muscular, anteriorly strongly widening duct; vasa deferentia joining the duct near its ental end. Spermathecae 3 pairs, in V, VI and VII, each with an ovoid strongly flattened ampulla and a short stout duct of about one third its length which is joined at the pore by a single, elongate clavate diverticulum, often bent through a large angle near its slender base, with spermatozoal iridescence; length right posterior spermatheca (straightened) = 1.5mm; ratio total length: length duct = 4.2; ratio length: length diverticulum (straightened) = 1.8.

ETYMOLOGY. Named for the type locality.

REMARKS. *T. carbinensis* shares with *T. montislewisi* (Jamieson, 1976), *T. barronensis* (Fletcher, 1887) and *T. raveni* (Jamieson, 1976) the presence of three pairs of spermathecal pores in 4/5, 5/6 and 6/7. The last two species differ from it in their long and tortuous spermathecal diverticula and location of the spermathecal pores in the vicinity of setal lines *d-e*. *T. montislewisi* is similar to *T. carbinensis* in having a short, clavate diverticulum uniting with the spermathecal duct at the body wall but the pores are more ventral, in line with the ventral setal couples (*ab*), and its prostate ducts are not as tortuous. The male porophores in *T. carbinensis* differ from those of *T. montislewisi* in appearing to be partly formed by evagination of the muscular prostate ducts.

***Terrisswalkerius mcilwraithi* sp. nov.**  
(Figs 33-36; 39)

TYPE LOCALITY. Peach Creek, McIlwraith Range, 13°44'17"S 143°20'15"E, alt. 500-520m, notophyll

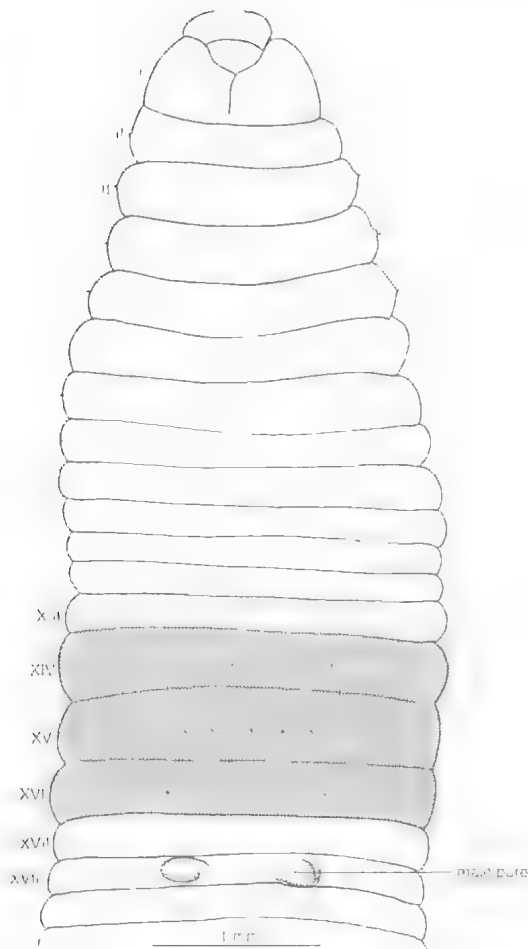


FIG. 33. *Terrisswalkerius mcilwraithi* sp. nov. Holotype, QMG211995. Ventral view of forebody and clitellar region.

vine forest with fan and feather palms, bank of creek, in loose upper horizon, on Kintore adamallite granite, K.R. McDonald, 26 & 27 Sep 1996.

**MATERIAL EXAMINED, HOLOTYPE.** (1) P1, used for SEM (+ immature non-type), QMG211996; P2-4 QMG211997-211999; P5, QMG212024 (used for DNA study); P6, QMG212037.

**DESCRIPTION.** Length 25 (P5), 31 (P3), 34mm (P2; holotype and paratype 1 are posterior amputees). Width (midclitellar) 2.0-2.3mm, wider in the forebody. Segments 125 (P4), 137 (P3), 139 (P2). Colour in life chocolate brown, darker anterior to the clitellum; pale brown ventrally; clitellum pinkish brown; in ethanol reddish brown, clitellum and ventral surface whitish.

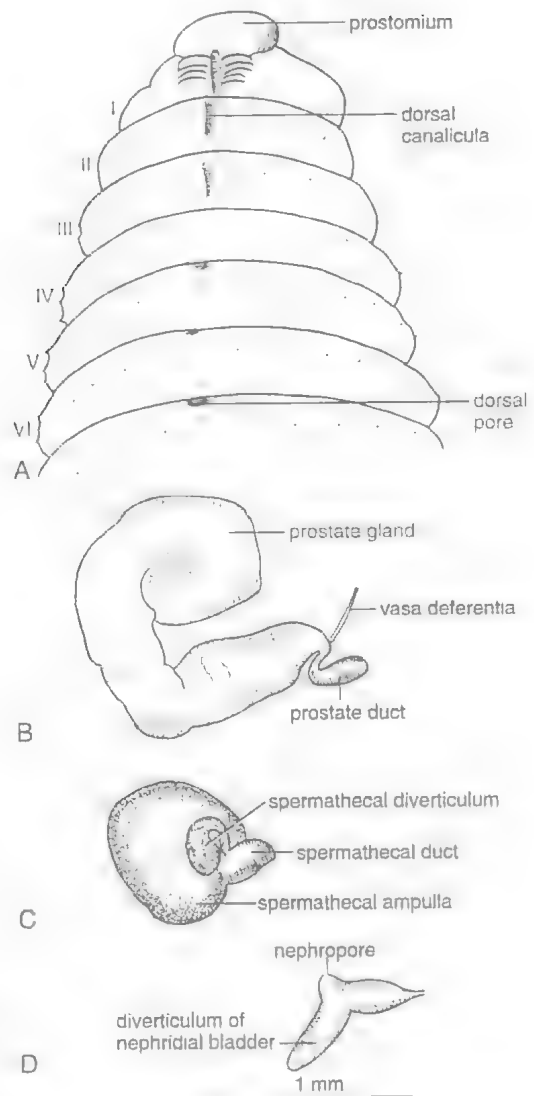


FIG. 34. *Terrisswalkerius mcilwraithi* sp. nov. Holotype, QMG211995. A, dorsal view in region of prostomium. B, left prostate. C, left spermatheca. D, left nephridial bladder of XX. A-D same scale.

**Behaviour:** saltatory by rapid 'flicking' movements when disturbed. Prostomium epilobous 1/3, broad, transversely elliptical; in the holotype giving the impression of being almost tanylobous owing to transverse plications of the peristomium posterior to it but this feature less obvious or absent in paratypes. A deep, wide dorsal canalicula or gauge bisects the peristomium dorsally and impinges on the posterior extremity of the prostomium; this groove is present segmentally



in II and III (but not intersegmentally) and a middorsal darker pigmented but not incised line is present throughout the postclitellar region. Peristomium not shortened, longer than segment II, with V-shaped midventral anterior indentation continuous with a midventral groove. First dorsal pore 4/5. Setae in XII 28 (H, P3), 36 (P2, P4); in XX 28 (P2), 30 (H), 32 (P3), 36 (P4); caudally (12 segments anterior to the posterior extremity) 36 (P4), 40 (H, P2), 42 (P3). The ventral break (*aa*) only slightly wider than the adjacent setal couple (*ab*); the dorsal break (*zz*) slightly less than twice the adjacent couple (*yz*); *ab* not significantly narrower than other intervals of the same side; setae *a* and *b* absent in XVIII; *a* line fairly straight throughout; *z* lines check. The setal surfaces are cicatrized as is common in earthworms. Nephropores visible in a straight series on the clitellum, lateral, in setal lines 10, anteriorly in their segments. Clitellum annular, XIII-XVII (paratypes 2 and 3) or weak in XIII and absent in XVII (H, P1); intersegmental furrows and setae retained; dorsal pores occluded. Male porophores a pair of scarcely protuberant whitish ellipses in XVIII centred slightly lateral of *b* lines (H, P1-3); a central male pore visible on each only in P2; the pores 0.5 mm apart. Accessory genital markings absent. Female pores on XIV, from internal investigation, but not visible externally. Spermathecal pores one pair, in 7/8, slightly lateral of *b* lines inconspicuous slits demonstrable only with difficulty by parting the intersegmental furrow, very approximately 0.7 mm apart.

Septa 12/13 and 13/14, slightly thickened, the remainder delicate. Last hearts in XII. Gizzard a large, glossy, firmly muscular, anteriorly slightly widening cylinder; anterior to septum 7/8 but segmental position indeterminable owing to extreme attenuation of septa by posterior projection of the gizzard. Very large pharyngeal glands, forming a lobe on each side, envelope the anterior region of the gizzard. Oesophagus vascular in X-XV; enlarged in XIV and XV in which it has a pair of large circumferential vessels connecting to the supraoesophageal vessel but no true calciferous glands present. Intestine commencing, with abrupt expansion, in XVII. Nephridia stomate vesiculate, exonephric holonephridia commencing in II; those in II tufted, but not large, and attached to the buccal cavity though enteronephry not proven; those in III only slightly tufted and like the remaining, simple nephridia, exonephric; bladders not demonstrable anterior to IV; those in the intestinal region conspicuous by virtue of an obliquely vertical, outwardly leaning sac on each

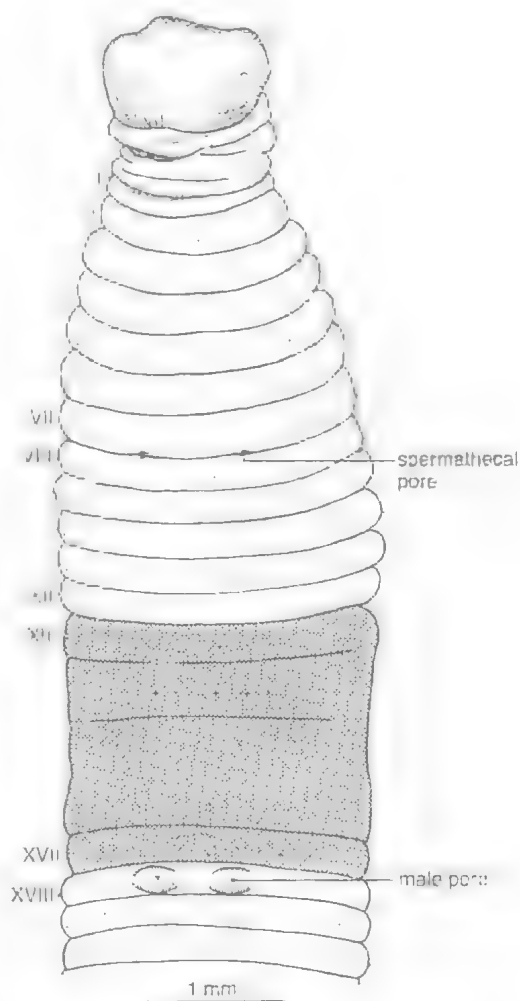


FIG. 35. *Terristwalkerius mcilwraithi* sp. nov. Paratype 2, QMG211997. Ventral view of forebody and clitellar region.

side which is the lateral diverticulum of each bladder and often has a brownish, chloragogenous appearance. Very large compacted sperm masses and well developed nacreous seminal funnels a pair in each of X and XI; seminal vesicles a pair of large elongate lobulated sacs in XII and a small pair in IX; no pseudo-vesicles in XIII. Small ovaries with few egg strings, and large oviducal funnels, in XIII; ovisacs absent. Prostates tubuloracemose, confined to XVIII, the gland a flattened band coiled one on itself in a horizontal plane, with the wide ental end anterior; duct moderately long, muscular, bent once and strongly widened ectally; vasa deferentia joining the gland shortly before its junction with the duct;

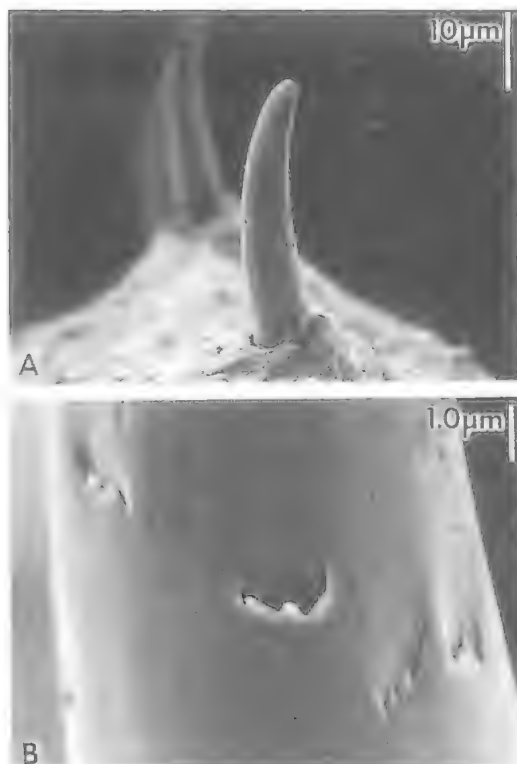


FIG. 36. *Terrisswalkerius mcilwraithi* sp. nov. Paratype 1, QMG211996. Scanning electron micrographs. A, a seta. B, sculpturing of same.

penial setae absent. Spermathecae one pair, with large, subspheroidal ampulla and clearly demarcated, stout, fusiform muscular duct; the comma-shaped uniloculate diverticulum, with spermatozoal iridescence, joining the junction of ampulla and duct; length left spermatheca = 0.8mm; ratio total length: length duct = 2.7; ratio length: length diverticulum (straightened) = 1.6 (H).

ETYMOLOGY. Named after the type-locality.

REMARKS. *Terrisswalkerius mcilwraithi* is closer morphologically to *T. blounti* than to other members of the genus and shares with it the otherwise unique restriction of the spermathecal pores to intersegment 7/8 (Table 1). In view of the close similarity of the two entities, and their relatively close geographical proximity, albeit separated by 3° of latitude, this location of the spermathecal pores is deduced to have developed in a common ancestor and is a synapomorphy of the two species. Of these, often subtle differences, the more significant, supporting specific separation of *mcilwraithi* from *blounti* appear to be the lack of closer coupling of the ventral setae

TABLE 1. Differences between *T. mcilwraithi* and *T. blounti*.

<i>Terrisswalkerius mcilwraithi</i> sp. nov.	<i>Terrisswalkerius blounti</i> (Jamieson, 1976)
Type Locality: 13°44'17"S	Type Locality: 16°34'S
Prostomium with middorsal groove only posteriorly	Prostomium bisected by middorsal groove
Setae: <i>ab</i> not narrower than other intervals of the same side	Setae: <i>ab</i> significantly narrower than other intervals of the same side
<i>aa</i> only slightly wider than the adjacent setal couple	<i>aa</i> ~2-4 <i>ab</i> (widest caudally)
<i>zz</i> slightly less than twice the adjacent couple	<i>zz</i> smaller than adjacent couple
Nephropores in setal lines 10	Nephropores in setal lines 5
Male porophores 0.5mm apart	Male pores 1mm apart
Spermathecal pores, slightly lateral of <i>b</i> lines, very approximately 0.7mm apart	Spermathecal pores between setal lines 3 and 4, 1.7-2.0mm apart
Septa 12/13 and 13/14, slightly thickened, the remainder delicate	Thickest septa 8/9-12/13, moderately thickened
Nephridia with diverticulate bladders	Nephridia lacking bladders
Prostates tubuloracemose, confined to XVIII, the gland a flattened band coiled one on itself in a horizontal plane	Prostates long, flattened and irregularly tubular (tubuloracemose), meandering with adpressed coils in XVII, XVIII-XXIV, XXII
Spermathecae with stout, fusiform muscular duct	Spermathecae with long, slender and twisted duct
Ratio total length spermatheca: length duct = 2.7	Ratio total length spermatheca: length duct = 1.7
Ratio length: length diverticulum (straightened) = 1.6	Ratio length: length diverticulum = 2.3

*a* and *b*; location of nephropores in setal lines 10 (not 5, though lateral in both species); the closer approximation of the spermathecal and male pores; the presence of nephridial bladders; and the restriction of the prostates to XVIII and their coiled, not tortuous, form.

The type-locality of this species is almost 2° of latitude north of previous records for the genus. Its habitat is notophyll vine forest with fan and feather palms (*Licuala ramsayi*, *Ptychosperma elegans*, *Calamus australis*, and *Archontophoenix* spp.) along drainage lines with moist, humic soils, on Kintore Adamallite granite.

It is found sympatrically with *Diploptrema attenuata*, *D. scheltingai*, *Neodiploptrema mcdonaldii*, and species yet to be identified.

***Terrisswalkerius miseriae* sp. nov.**  
(Figs 37-39)

TYPE LOCALITY. 15°52'S 145°13'E (1'x1' grid), Mt Misery, S.W. slope, Timber Reserve 165 Monkhouse, under logs, notophyll vine forest, alt. 600-750m. K.R. McDonald, C. Schneider, J. Sumner, 11 Nov 1994.

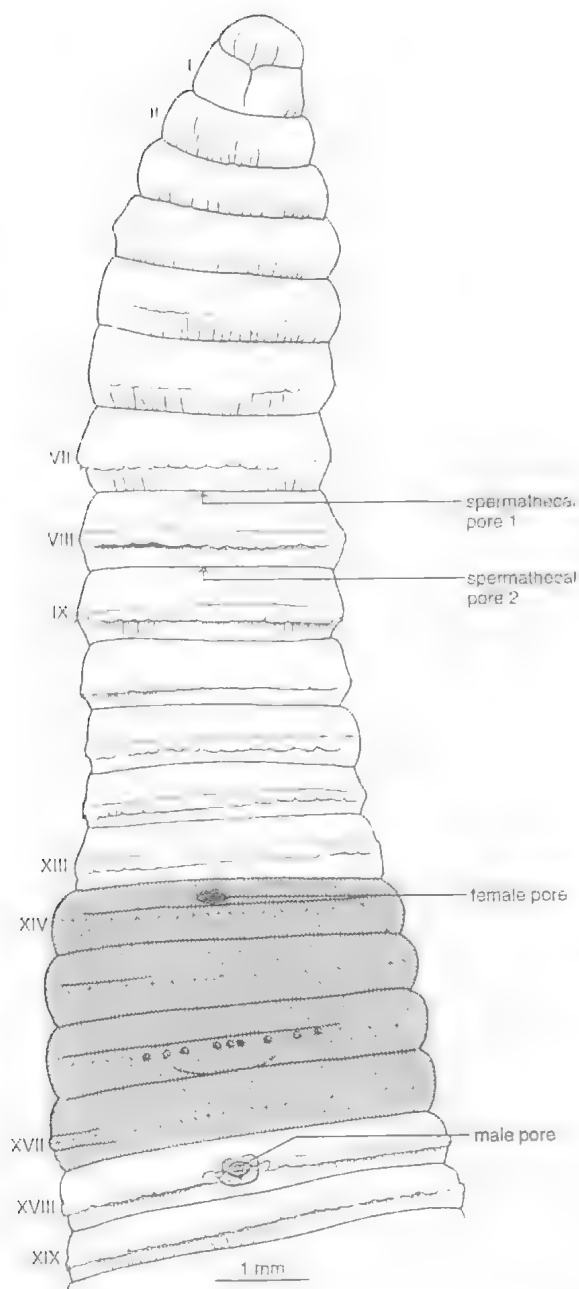


FIG. 37. *Terrisswalkerius miseriae* sp. nov. Holotype, QMG211964. Ventral view of forebody and clitellar region.

**MATERIAL EXAMINED.** HOLOTYPE, QMG211964. PARATYPES, P1 and 2, QMG211965-66. OTHER MATERIAL, 3 immature specimens not designated types.

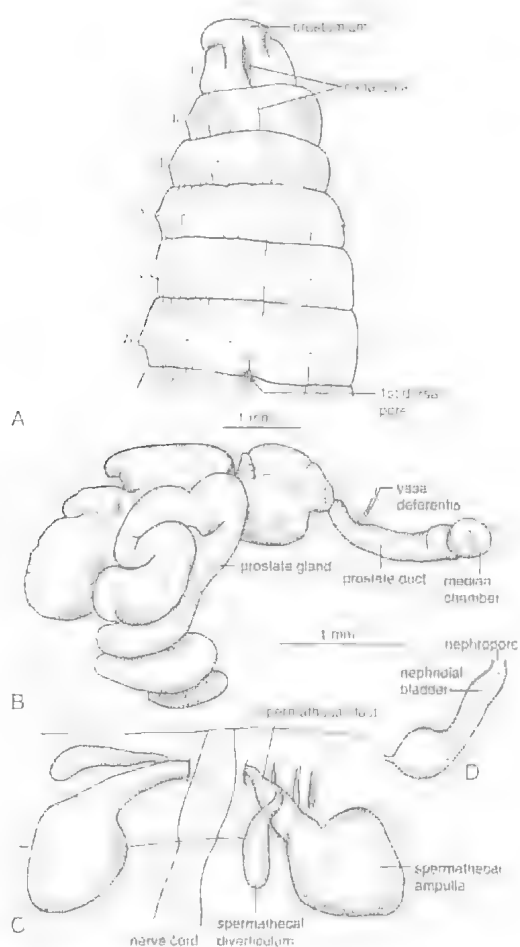


FIG. 38. *Terrisswalkerius miseriae* sp. nov. Holotype, QMG211964. A, dorsal view in region of prostomium. B, left prostate. C, spermathecae of IX, *in situ*. D, right nephridial bladder of VIII. B-D same scale.

**DESCRIPTION.** Length 48-70mm; H 54mm. Width (midclitellar) 3-(H)5mm (H). Segments 97-111; H 94. Colour in ethanol purplish brown, pale ventrally; clitellum buff. Prostomium epilobous 1/2, dorsal tongue open, sides parallel or slightly concave; a wide, deep, middorsal groove bisecting the peristomium and continuing posteriorly as a narrow groove (canalicula) which more distinct in the postclitellar region. Peristomium bifid ventrally. First dorsal pore 6/7. Setae 31 in XII; 40 caudally (12 segments from posterior end); all rows approximately straight. In XII, *aa*: *ab*: *bc*: *cd*: *yz*: *zz* = 1.0: 1.0: 1.5: 1.1: 3.0: 4.5; no ventral break; dorsal break ca. 1 to 3 times the adjacent interval. Nephropores conspicuous from V posteriorly, near the anterior borders of their

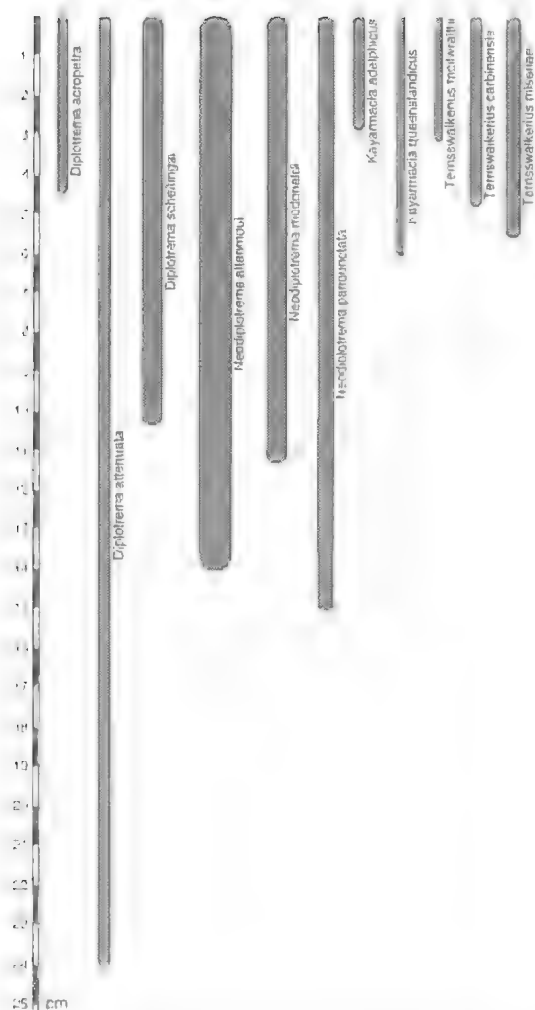


FIG. 39. Relative sizes of the oligochaete species described in this paper.

segments, in a slightly dorsolateral straight line on each side, with rare irregularity in single segments; much less conspicuous behind the clitellum; those on the clitellum in setal lines 10 from the ventrum. Clitellum annular, XIV-XVII; setae, nephropores, dorsal pores and intersegmental furrows retained. Male pore, in XVIII, in a midventral transverse slit on very small transversely elliptical whitish papilla centred shortly anterior to the setal arc and not extending posteriorly to this, surrounded by a narrow, rounded oblong, low pad which is subdivided into two anterior and two posterior quarters. Genital markings absent. Female pore single, midventral, midway between the setal arc and anterior margin of XIV.

Spermathecal pores unpaired, midventral, in 7/8 and 8/9, inconspicuous, concealed in the intersegmental furrow but succeeded by an indistinct whitish spot at the anterior border of the succeeding segment.

Septa 10/11-13/14 the thickest, but not strongly thickened. Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XII. Gizzard very large, an elongate, glossy, muscular, anteriorly widening cylinder; in V but septum 5/6 very delicate and displaced, funnel-like, posteriorly, the posterior end of the gizzard being at the level of segment IX. Oesophagus in VII-XI segmentally swollen and whitish, increasing in width throughout these segments; broadly tubular in XII-XVII; calciferous glands absent. Intestine thin-walled, commencing with abrupt expansion in XVIII(?). Nephridia stomate, vesiculate, holonephridia, with large preseptal funnel and simple, elongate pyriform bladder. Fan-like testes and large iridescent sperm funnels two pairs, free in X and XI. Ovaries large, palmate, and funnels in XIII; ovisacs not seen. Prostates a pair, in XVIII-XXI, each unusually coiled; the ectal half almost racemose, the ental half thickly tubular; a flaccid, thin-walled duct, lacking muscular sheen, passing medianly to join the lateral aspect of a small midventral rounded chamber, not forming a noticeably muscular bursa, at the pore; conjoined vasa deferentia joining the duct at about its ectal fourth. Spermathecae 2 pairs, each with ovoid ampulla and slender duct of approximately the same length which is joined at approximately its ental third by a digitiform diverticulum about as long as the duct; the spermathecal duct entering the body wall anterior to setae *a* but presumably fusing with its fellow before opening at the common pore.

ETYMOLOGY. For the type locality.

REMARKS. *Terrisswalkerius miseriae* completes the trend to midventral approximation of the spermathecal and male pores which is evident in several other species of *Terrisswalkerius*. Total fusion of the pores, seen in this species, has hitherto been a diagnostic character of *Fletcherodrilus*. However, *Fletcherodrilus* remains distinct in having unpaired spermathecae, each with a pair of diverticula which are reasonably deduced to be retained from the single diverticulum of each member of an original pair of spermathecae. In *T. miseriae* the spermathecae, although opening at a single pore, are paired. There are three or five spermathecal pores in *Fletcherodrilus*, contrasting with two in *T. miseriae*.

Fletcher (1889), describing the type specimens of *Fletcherodrilus*, the type-species of its genus, claimed to have observed a stage in reduction of paired spermathecae, each of the pair with a single diverticulum, and with one of the ampullae rudimentary, to the unpaired condition seen in all species of the genus. Despite this evidence for origin of *Fletcherodrilus* from a form with paired spermathecae, an origin which would be presumed, as above, even in the absence of the exceptional individuals, the view is here maintained that *Terrisswalkerius miseriae* is not more closely related to *Fletcherodrilus* than it is to other species of *Terrisswalkerius* within what has been shown cladistically (Jamieson, 1994) to be a monophyletic *Fletcherodrilus*-*Terrisswalkerius* assemblage. A further difference of *T. miseriae* from *Fletcherodrilus* is absence of calciferous glands. It also lacks the pleated anterior genital markings which are a novelty of some species of *Fletcherodrilus* (*F. menurus* and *F. sigillatus*) though these markings possibly were not present in the stem form of *Fletcherodrilus*, being unknown in the type-species, *F. unicus*, or in *F. affinis* and *F. fasciatus*. Relationships of *T. miseriae* are the subject of a cladistic study of mitochondrial DNA which is in progress.

## DISCUSSION

In the above account, ten new species, in four genera, have been described from the Cape York Peninsula, Queensland: *Diploptrema attenuatus* sp. nov.; *D. scheltingai* sp. nov.; *Neodiploptrema medonaldi* sp. nov.; and *Terrisswalkerius mcilwraithi* sp. nov., from the McIlwraith Range; *Diploptrema acropetra* sp. nov., *Neodiploptrema altanmonii* sp. nov., *N. paripunctata* sp. nov., and *Kayarmacia adelphicus* gen. et sp. nov., from Cape Melville National Park; *Terrisswalkerius carbinensis* sp. nov. from Mt Carbine Tableland, and *T. miseriae* sp. nov., from Mt Misery, near the headwaters of the Normanby River. *Kayarmacia queenslandicus* (Michaelsen, 1916) is redescribed from the Alice-Mitchell R. National Park, near the type-locality; it is clearly the sister-taxon of *K. adelphicus*.

These and other oligochaete species do not show congruence with the biogeographical affinities of various areas of Australia proposed by Crisp et al. (1995) in a cladistic analysis of the distribution of 11 angiosperm groups. Thus, of some 25 or more Australian oligochaete genera, *Begemius* Easton (1982) is the only indigenous genus which is also found in New Guinea, so far

as is known, whereas those authors recognize a close relationship between southern New Guinea and the Australian mainland. The genus *Diploptrema*, of which species are described in the present paper, has its closest relative, *Acanthodrilus*, in New Caledonia (Jamieson & Bennett, 1979) and these are in turn very closely related to eastern North American acanthodrilines, some of which may be referable to *Diploptrema* (see James, 1990). It appears that the Australian *Diploptrema* represent a Gondwanan and possibly Pangaeian acanthodrilid stock. The other Australian acanthodrilids described would previously have been attributed to the genus *Rhododrilus*, following Michaelsen (1916), but that they are congeneric with the predominantly New Zealand species, and the type-species, *R. minutus* Beddard (1889), is not here supported and the new genus *Kayarmacia* is erected to receive them. No acanthodrilids are known from New Guinea.

The genus *Neodiploptrema*, erected by Dyne (this volume) for species in the north-west of Cape York Peninsula and Thursday Island, is here shown to occur sympatrically with *Diploptrema* on the eastern side of the peninsula, at Cape Melville and in the McIlwraith Range. It is distinguished from *Diploptrema* by the meronephric condition and is reasonably considered by Dyne to have been derived by the supervation of this condition on the holonephry of *Diploptrema*. On this basis erection of *Neodiploptrema* would leave a paraphyletic *Diploptrema* unless, as seems improbable, the two genera are sister-taxa. There are, indeed, some indications that the *Neodiploptrema* condition was derived locally from that of *Diploptrema*, as is seen in the similarity of *N. medonaldi* to *D. ridei* Jamieson & Dyne (1976), from Cape York and Melville Island. However, there is no particular reason to believe that acquisition of meronephry in *Neodiploptrema* was a monophyletic event and the genus may well be polyphyletic from within *Diploptrema*. On strict cladistic principles *Diploptrema* and *Neodiploptrema* appear to form a monophylum and splitting of this into two genera thus is probably artificial, though convenient.

There remains, however, a possibility that origin of meronephry in *Neodiploptrema* was not temporally confined to Australia but that it may have been a more ancient event which occurred in a larger, Gondwanan or even Pangaeian area. The similarity of *Neodiploptrema* to the species of *Dichogaster*, itself a congeries, in Africa, central America and Asia might, if this were the case, be

an indication of close relationship of *Neodiploptrema* and the acanthodrilids with those Dichogastrini which, like *Dichogaster* (though not the sexprostatic Fijian type-species, *D. damonis* Beddard), have the acanthodriline arrangement of male pores. The occurrence of true calciferous glands in *Neodiploptrema mcdonaldi* adds to the remarkable similarity of this species to *Dichogaster*, notwithstanding the diploptreman affinities mentioned above. Although at present there is no firm reason to doubt local derivation of *Neodiploptrema* from *Diploptrema* these alternative affinities must be considered in further studies. Molecular studies which may shed light on the phylogenetic relationships of these and other genera are in progress.

Three species are here added to *Terrisswalkerius*. This genus occurs in and near the Wet Tropics of north Queensland, though there are grounds for considering relationship to Indian species (see Jamieson, 1977) at present placed in the plesiomorphic congeries known as *Diporochaeta*. *Terrisswalkerius* shows no close affinity to Australian species of *Diporochaeta* or to the type-species of that genus, and its congeners, in the New Zealand (see Jamieson, 1994). There is no indication in the distribution of *Terrisswalkerius* in the Wet Tropics of Queensland to suggest that the Atherton Tableland has closer biogeographic affinities with more southerly areas of E Australia, postulated for angiosperms by Crisp et al. (1995), than with other areas of the wet tropics. Nevertheless, the genus *Fletcherodrilus* which forms a monophylum with *Terrisswalkerius* (see Jamieson, 1994) has a distribution which is both sympatric with *Terrisswalkerius* and includes eastern Australia as far south as N New South Wales.

#### ACKNOWLEDGEMENTS

The author is grateful to those who collected or aided in collection of material described in this paper: L.A. Jackson, P.J. Lethbridge, K.R. McDonald, A.J. Stewart and W.E. Martin. It is impossible to adequately thank Keith McDonald for his incomparable collections and for the encouragement which he has given the author. David Schellinga and Lina Daddow gave valued technical assistance. All illustrations are by the author. This study was made possible by ABRIS and ARC grants to the author.

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NEW SPECIES OF PTERIIDAE, PINNIDAE, VENERIDAE, EUCIROIDAE AND CORBULIDAE FROM AUSTRALIA (MOLLUSCA: BIVALVIA: VENEROIDA).

KEVIN L. LAMPRELL AND JOHN M. HEALY

Lamprell, K.L. & Healy, J.M. 1997 06 30: New species of Pteriidae, Pinnidae, Veneridae, Euciroidae and Corbulidae from Australia (Mollusca: Bivalvia: Veneroidea). *Memoirs of the Queensland Museum* 42(1): 271-281, Brisbane. ISSN 0079-8835.

Seven new species of bivalves from Australia are figured and described: *Pteria howensis* sp. nov. and *P. cooki* sp. nov. (Pteriidae); *Atrina (Servatrina) palmensis* sp. nov. (Pinnidae); *Dosinia carpentariana* sp. nov. (Veneridae); *Euciroa queenslandica* sp. nov. (Euciroidae); *Corbula (Serracorbula) moretonensis* sp. nov. and *C. (Anisocorbula) stephensoni* sp. nov. (Corbulidae). All species are from Queensland except *Pteria howensis*, which is known only from Lord Howe Island. □ Mollusca, Bivalvia, Veneroidea, Australia.

Kevin L. Lamprell, Malacology Section, Queensland Museum, PO Box 3300 South Brisbane, Queensland, 4101, Australia; John M. Healy, Department of Zoology, University of Queensland, Queensland, 4072, Australia; 1 May 1997.

During the preparation of the second volume of 'Bivalves of Australia' (Lamprell & Healy, in prep.) a number of apparently unnamed species were uncovered in the collections of the Australian Museum (Sydney), the Queensland Museum (Brisbane) and that of one of the authors (Lamprell Collection). These species include representatives of the following genera/subgenera and families: *Pteria* (Pteriidae), *Atrina* (*Servatrina*) (Pinnidae), *Dosinia* (Veneridae), *Euciroa* (Euciroidae) and *Corbula* (*Anisocorbula* and *Notocorbula*) (Corbulidae). After searching the relevant literature, especially that pertaining to the Australian region (including Iredale, 1939; Lamy, 1941; Hynd, 1954; Takemura & Okutani, 1958; Rosewater, 1961; Fischer-Piette & Delmas, 1967; Healy & Lamprell, 1992; Lamprell & Whitehead, 1992; Lamprell & Stanisic, 1996; Poutiers & Bernard, 1995) and after comparisons with type specimens held in the Natural History Museum, London, the Muséum national d'Histoire Naturelle, Paris and the Department of Malacology, Zoological Museum of the University of Amsterdam, we were satisfied that our species should be described as new.

#### MATERIAL AND METHODS

All measurements were made using vernier dial calipers. Shell height given is from the umbones to the ventral margin on the left valve vertical to the hinge line. Shell length given is the greatest distance from anterior to posterior margin. Shell depth given is the greatest distance between the surfaces of the left and right valves. Shell size given is for the largest specimen examined by the authors unless otherwise stated.

Abbreviations used: AMSC = Australian Museum, Sydney; KL = Lamprell Collection; QMMO = Queensland Museum, Brisbane; WAM = Western Australian Museum, Perth; lv = left valve; rv = right valve; pv = paired or conjoined valves; NSW = New South Wales; NT = Northern Territory; Qld = Queensland.

#### SYSTEMATICS

The systematic arrangement used for each family herein follows that of various authors (Cox & Hertlein, 1969; Hertlein & Cox, 1969; Keen, 1969a,b) in the Treatise on Invertebrate Paleontology with the exception of the Euciroidae which follows Poutiers & Bernard (1995) and the Pinnidae which follows Rosewater (1961).

#### Family PTERIIDAE Gray, 1847

##### *Pteria* Scopoli, 1777

TYPESPECIES. *Mytilus hirundo* Linnaeus, 1758; SD-Kennard, Salisbury & Woodward, 1931.

##### *Pteria howensis* sp. nov. (Fig. 1A-H)

ETYMOLOGY. For Lord Howe Island.

DESCRIPTION. Shell length to 40.0mm; moderately solid, obliquely ovate, dorsal margin straight, umbones extend above the dorsal margin; both valves convex, left much more so and encompassing the right; a well-defined, rounded fold extends from the umbones to the postero-ventral margin. Anterior wing short, moderately deep from the hinge line to the narrow byssal



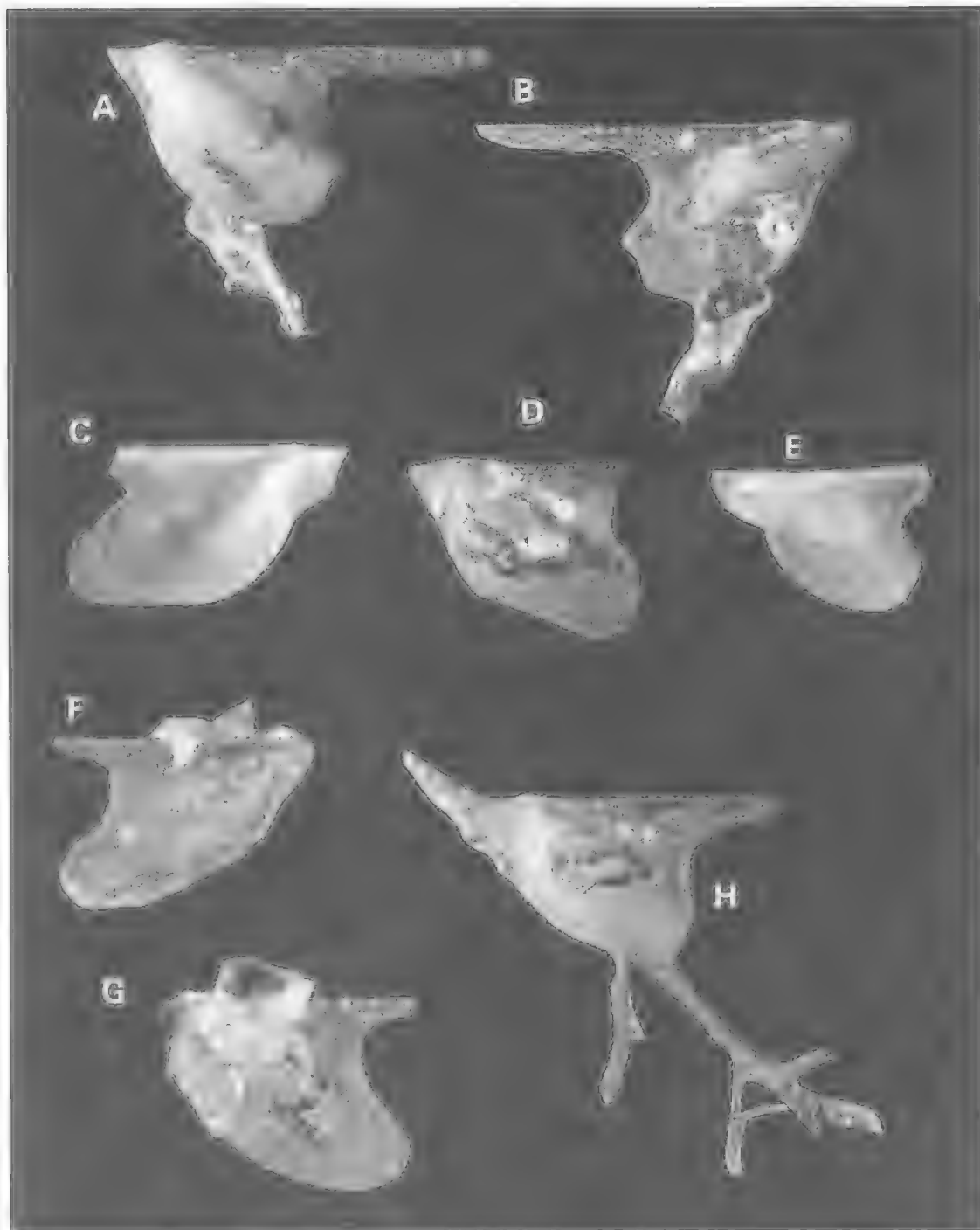


FIG. 1. *Pteria howensis* sp. nov. A-B, holotype; C-H, paratypes. A, external view of lv; B, external view of rv; C, internal view of lv; D, external view of lv; E, internal view rv; F, external view of rv; G, external view of lv; H, external view of lv.



notch; posterior wing narrow, varying from short to very long; anterior margin convex, posterior margin concave. Sculpture of concentric growth striae; periostracum of widely spaced, imbricated concentric lamellae. Colour externally light bronze with irregular, darker brown zigzag concentric patterns and concentric lines and an irregular black stripe on the umbonal fold; internally silvery nacreous, medially with a narrow pale brown margin.

**MATERIAL EXAMINED.** HOLOTYPE: AMSC-70584, 1pv, off Ball's Pyramid, Lord Howe I. 55m, McIntyre, 22.11.1960. Length 40.0mm, height 18.5mm, depth of conjoined valves 6.5mm. PARATYPES: AMSC203159, 3pv, 1lv, same data as holotype. Length of largest paratype 27.8mm, height 19.6mm, depth of conjoined valves 7.8mm.

**HABITAT AND DISTRIBUTION.** Attached to soft corals in shallow water; known only from Lord Howe Island.

**REMARKS.** *Pteria howensis* sp. nov. is similar to *P. peasei* (Dunker, 1872), *P. sibogae* Prashad, 1932, *P. loveni* (Dunker, 1872) and *P. cypsellus* (Dunker, 1872) in outline, but does not attain the large size of these species. Additionally none of the latter species have the consistent bronze colour evident in *P. howensis*. *P. penguin* (Röding, 1798) and *P. fulcata* (Lamarck, 1819), while similar in shape, are much heavier-shelled species than *P. howensis* and also attain a much larger size. *P. howensis* is similar in shape to juvenile specimens of *P. penguin* and *P. fulcata*, but differs in colour. Both these species retain the same colour to adulthood. *P. howensis* in both juvenile and adult has a consistent light bronze background shell colour, (black in *P. penguin* and bone-green in *P. fulcata*) with brown, irregular zigzag concentric patterns and irregular concentric lines over the surface and an irregular black stripe on the umbonal fold.

***Pteria cooki* sp. nov.**  
(Fig. 2A-D)

**ETYMOLOGY.** For Stephen Cook.

**DESCRIPTION.** Shell length to 52.5mm; fragile, translucent, elongate, obliquely ovate, dorsal margin straight, umbones extending above margin line; both valves convex, left much more than the right. Anterior wing more or less an extension of the dorsal margin with a strong oblique depression or fold separating it from the main body; posterior wing moderately short with an almost

obsolete fold separating it from the main body of the shell. Sculpture of concentric microscopic striae; periostracum of widely spaced, narrow radial processes arranged in concentric rows, parallel to the shell lip. Colour externally off-white to pearl-white with a strong radial brown ray extending from the umbones to the posteroventral margin, stronger on the lv, weaker and sometimes obsolete on the right, with a narrow brown stain extending the full length of the dorsal margin; internally nacreous medially with a wide translucent white margin.

**MATERIAL EXAMINED.** HOLOTYPE: QMMO59356, 1pv, Shelburne Bay, north Qld, 11°27'S, 142°55'E, 18m, S. Cook, May 1992. Length 54.2mm, height 20.0mm, depth of conjoined valves 3.6mm. PARATYPES: AMSC203157, 3pv, WAM46.97, 1pv, same data as holotype; AMSC320793, 1pv, 11°13.2'S, 143°25.8'E, Shelburne Bay, north Qld, 22m, S. Cook, Apr 1993. Dimensions of paratypes: AMSC203157, length 52.5mm, height 23.5mm, depth of pv 9.5mm; WAM46.97, length 51.3mm, height 24.5mm, depth of pv 10.0mm. OTHER MATERIAL: KL, 3pv, same data as holotype; QMMO59357, 1pv, Arafura Sea, stn 511, attached to sea anemone, Bureau of Fisheries, K. Colgan, 1989; QMMO59358, 11pv, Arafura Sea, stn 524, attached to sea anemone, Bureau of Fisheries, K. Colgan, Nov 1989; QMMO59359, 1pv, Arafura Sea, stn 541, attached to sea anemone, Bureau of Fisheries, K. Colgan, Nov 1989; QMMO59360, 2pv, Arafura Sea, stn 505, attached to sea anemone, Bureau of Fisheries, K. Colgan, Nov 1989; QMMO59361, 1pv, Arafura Sea, stn 403, attached to sea anemone, Bureau of Fisheries, K. Colgan, Nov 1989; QMMO59362, 1pv, Arafura Sea, stn 531, attached to sea anemone, Bureau of Fisheries, K. Colgan, Nov 1989.

**HABITAT AND DISTRIBUTION.** Attached to sea anemones and soft corals to 22m; *Pteria cooki* appears restricted to north Qld and the Northern Territory, presently known from Shelburne Bay on the east coast of Cape York and the Arafura Sea.

**REMARKS.** *P. cooki* sp. nov. differs from *P. levitata* Iredale, 1939 principally in colour: *P. cooki* being pearly white with a dark brown zigzag pattern and oblique rays whereas *P. levitata* has a dark brown, heavily mottled shell with obscure oblique rays and with no trace of nacreous lustre. *P. levitata* is also more solid, attains a larger size and has more pronounced hinge teeth. *P. cooki* occurs sympatrically with *P. brevisulcata* (Dunker, 1872) but can be distinguished from that species by having a lighter shell, weaker sculpture and shorter wings. The brown dorsal margin and ray, constant in *P. cooki* is absent in *P. brevisulcata*.

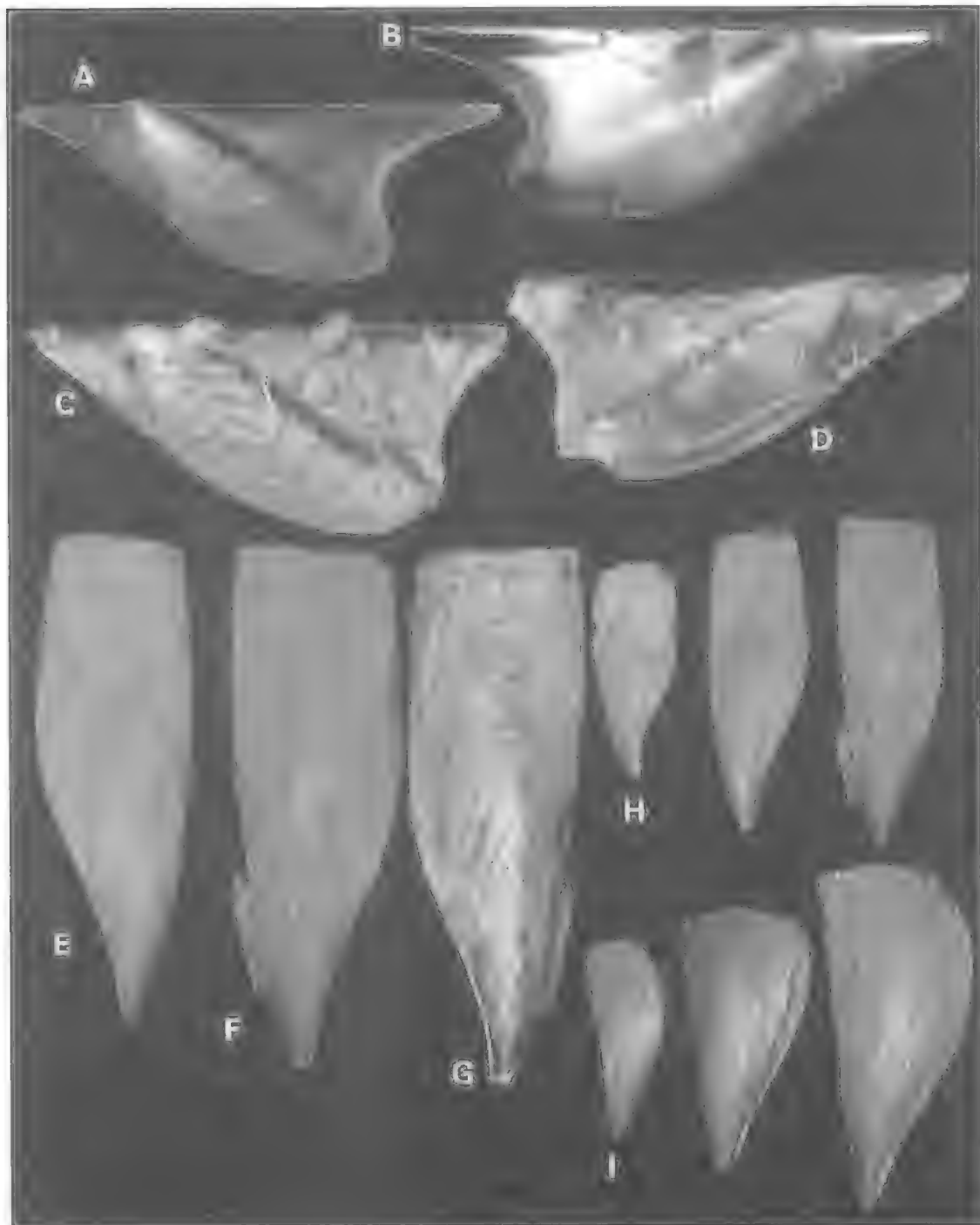


FIG. 2. A-D, *Pteria cooki* sp. nov. A-B, holotype; C-D, paratypes. A, external view of lv; B, internal view of lv; C, external view of lv; D, view of pv shown principally from rv aspect. E-G, *Atrina (S.) palmensis* sp. nov. E, external view of rv of holotype; F, external view of lv of paratype; G, internal view of lv of paratype; H, growth series *A. (S.) palmensis* (left to right: lv's paratype, holotype, paratype); I, *Atrina (S.) pectinata*: three juvenile specimens (dredged from same locality as *A. (S.) palmensis*).

## Family PINNIDAE Leach, 1819

*Atrina* Gray, 1842

TYPE SPECIES. *Atrina vexillum* (Born, 1778); SM-Gray, 1847.

*A. (Servatrina)* Iredale, 1939.

TYPE SPECIES. *Atrina assimilis* (Reeve, 1858).

*Atrina (Servatrina) palmensis* sp. nov.  
(Fig. 2E-H)

ETYMOLOGY. For Palm Island.

DESCRIPTION. Shell to 51.6 mm in height; thin, relatively small for family. Valves equivalve and inequilateral, profiles triangular anteriorly and quadrate posteriorly. Both valves well inflated in proportion to the shell size. Dorsal margin of each valve conspicuously convex; ventral margin straight posteriorly, concave anteriorly; posterior margin truncate, forming a right angle with the posteroventral margin; ligament extending approximately half the length along the dorsal edge from the umbones. Sculpture of well-defined, narrow ribs (10 ribs/cm measuring from the ventroposterior margin), curving strongly towards the ventral edge, ornamented with fine erect scales which are sparse on the dorsal surface, stronger and more numerous on the ventral surface and obsolete towards the umbones; internally ribs are impressed as deep grooves. Colour externally horn with purple-black umbonally; internally the nacreous surface covers the anterior half of the shell.

MATERIAL EXAMINED. HOLOTYPE: AMSC-203160, 1pv, between Palm and Curacao Islands, north Qld, dredged, 9m, K. Lamprell & P. Spoor, Nov 1990. Height 47.5 mm, width from dorsal to ventral margins 15.1 mm, width of pv 8.9 mm, PARATYPES: AMSC203161, 1pv, same data as holotype. Height 33.5 mm, width from ventral to dorsal margins 12.6 mm, width of pv 7.2 mm; QMMO59355, 1lv, 1 broken rv, off Palm I, north Qld, dredged, K. Lamprell & P. Spoor, 1989. Height 51.6 mm, width from dorsal to ventral margins 16.5 mm, depth of lv 4.5 mm.

HABITAT AND DISTRIBUTION. Dredged to 9m in sandy, weed-covered areas; between Palm and Curacao Islands, north Qld.

REMARKS. *Atrina (S.) palmensis* sp. nov. appears to live shallowly anchored to a sandy, weed-covered bottom in the Palm-Curacao Island passage. Freshly collected specimens occasionally showed traces of byssal threads (Lamprell

pers. obs.), although these threads are not preserved in any of the specimens from the type series.

Juvenile as well as large specimens of *A. (S.) pectinata* were also dredged from the same locality sometimes occurring in the same dredge haul as specimens of *A. (S.) palmensis*. However even as very small juveniles, these two species can be readily separated on the basis of valve profile and external sculpture. Whereas *A. (S.) pectinata* exhibits marked variation in the number of ribs and degree of ornamentation (Fig. 1), *A. (S.) palmensis* is remarkably constant in its sculpture. *Atrina (S.) palmensis* compared with the holotype of *A. (S.) penna* (Reeve, 1858) held in the Natural History Museum, London (BMNH 1252.8.29.41.3) from the Indonesia-Philippines area, which exhibits a similar narrow valve profile, differs in the dorsal edge (hinge) and ribs being curved towards the posteroventral margin (not curved in *A. (S.) penna*) while the ribs in *A. (S.) palmensis* are densely ornamented with low scales, the ribs in *A. (S.) penna* have strong, raised scales medially to the dorsal edge and obsolete to the ventral edge.

## Family VENERIDAE Rafinesque, 1815

*Dosinia* Scopoli, 1777

TYPE SPECIES. *Venus concentrica* Born, 1778; *fide* Fischer-Piette, 1942; M.

*Dosinia carpentariana* sp. nov.  
(Fig. 3A-E)

ETYMOLOGY. For the Gulf of Carpentaria.

DESCRIPTION. Shell length to 38.5 mm; ovate, equivalve, moderately inflated, solid; umbones prosogyrate; lunule heart-shaped, raised centrally, strongly impressed peripherally, surrounded by the lamellate ends of the concentric, principal ribs continue on the lunule as lamellae; escutcheon long, narrow, defined by a raised, spinose ridge; ligament impressed; anterodorsal margin short, convex, sloping, widely rounded at the anterior margin; posterodorsal margin convex, sloping, becoming widely rounded at the posterior margin; ventral margin evenly and widely convex. Sculpture of numerous, strong, widely spaced, concentric ridges which become lamellose at the antero- and posterodorsal margins, interstices with 4-6 minor concentric ridges. Ligament long narrow, brown in colour. Hinge plate broad. Hinge of lv with anterior lateral tooth

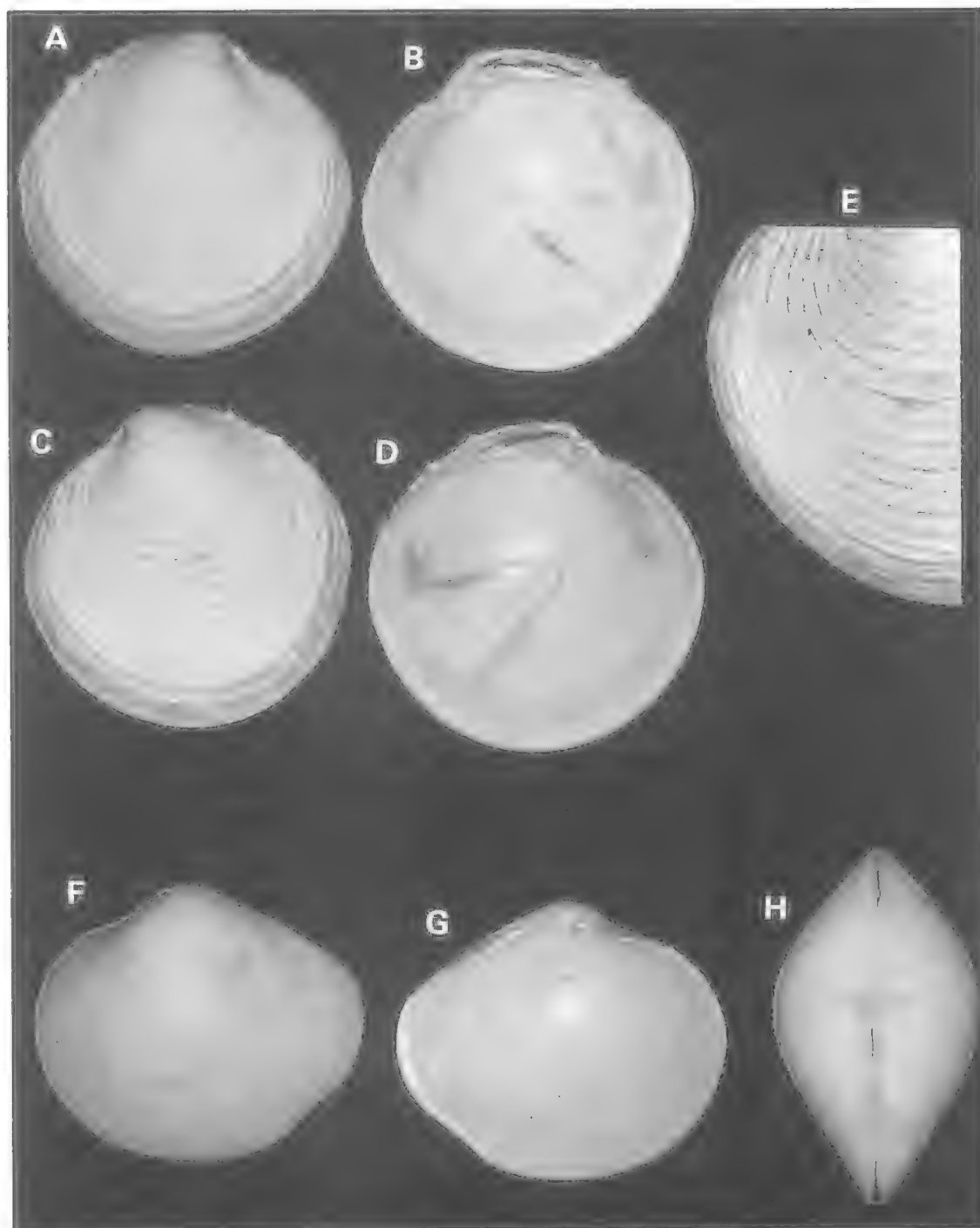


FIG. 3. A-E, *Dosinia carpentariana* sp. nov. A, B, external and internal views of rv of holotype; C, D, external and internal views of lv of holotype; E, detail of primary and secondary concentric growth ridges. F-H, *Euciroa queenslandica* sp. nov. F, G, external and internal views of lv of holotype; H, dorsal view of pv showing umbones, lunule and extent of valve inflation.

small, knob-like, bifid; anterior cardinal blade-shaped, raised, slightly oblique; median cardinal thin, posteriorly oblique; posterior cardinal thin, oblique, parallel to median cardinal. Hinge of rv with socket to accommodate anterior lateral of lv; anterior cardinal short, joined at apex with moderately solid, oblique, raised, median cardinal; posterior cardinal thin, raised, oblique. Muscle attachment scars well defined, anterior adductor scar narrow, elongate; posterior adductor scar rear-drop shaped, Pallial line line. Pallial sinus deep, slightly angulate terminally, ascending, extending beyond shell median. Colour internally and externally chalk-white; periostracum grey.

**MATERIAL EXAMINED.** HOLOTYPE: QMMO-59363, 1pv, Gulf of Carpentaria, 10°30'S, 137°12.1'E, S. Cook, 50m, 19 Nov 1990. Length 27.0mm, height 26.4mm, width of pv 13.3mm. PARATYPES: AMSC107105, 3lv, Gulf of Carpentaria, 12°42.5'S, 141°31.7'E, 18m; AMSC123934, 1lv, 14°30'S, 141°20.5'E, NW of Edward River, Gulf of Carpentaria, Coll. I. Loch, 14.6m, 1976; AMSC304562, 1lv, NW of Edward River, Gulf of Carpentaria, 14°46'S, 141°20.7'E, 18m, I. Loch, 1976; AMSC107040, 24lv, 26rv, off Albert River mouth, Gulf of Carpentaria, 17°24'S, 139°47'E, D.F. McMichael & J.C. Yaldwyn, 1963; AMSC107014, 8lv, 10rv, off Albert River mouth, Gulf of Carpentaria, 17°24'S, 139°47'E, D.F. McMichael & J.C. Yaldwyn, 4-9m, 1963; AMSC123102, 1rv, W of Nassau River, E Gulf of Carpentaria, 15°51'S, 141°21'E, CSIRO, 7.3m. Dimensions of largest paratype (AMSC107105): Length 38.5mm, height 39.6mm, width 10.2mm.

**HABITAT AND DISTRIBUTION.** Trawled and dredged to 50m in sandy mud; known only from the Gulf of Carpentaria.

**REMARKS.** *Dosinia carpentariana* sp. nov. cannot be confused with any other known Indo-Pacific *Dosinia* because of its distinctive sculpture of numerous, strong, widely spaced, concentric ridges, whose interstices have 4-6 minor concentric ridges. Other species occurring in northern Australia are *D. amphidesmoides* (Reeve, 1850), *D. histrio* (Gmelin, 1790), *D. sculpta* (Hanley, 1845), *D. amina* Iredale, 1930, *D. tumida* (Gray, 1838), *D. mira* Smith, 1885, *D. exasperata* (Philippi, 1847), *D. lochi* Healy & Lamprell, 1992, *D. queenslandica* Healy & Lamprell, 1992 and *D. laminata* (Reeve, 1850), all of which have narrow, concentric interstices, without interstitial riblets; *D. kaspiensis* Fischer-Piette & Delmas, 1967 which has very fine concentric lirae with faint, central radial threads; *D. alenai* Fischer-Piette & Delmas, 1967, *D. juvenilis* (Gmelin, 1791), *D. scalaris* (Menke, 1843) and *D. contusa*

(Reeve, 1850) which have wide concentric ridges and narrow interstices and *D. incisa* (Reeve, 1850) which has coarse, concentric ridges with obscure radial ridges medially.

#### Family EUCIROIDAE Dall, 1895

##### *Euciroa* Dall, 1881

**TYPE SPECIES.** *Verrucordia elegantissima* Dall, 1881 M

##### *Euciroa queenslandica* sp. nov. (Fig. 3F-H)

**ETYMOLOGY.** For Queensland

**DESCRIPTION.** Shell to 42.3mm in length; light weight but moderately solid; moderately inflated, equivalve, with an obscure, oblique ridge posteriorly, preceded by a shallow oblique flexure, slightly gaping posteriorly. Anterior margin short, almost straight, widely rounded terminally; posterior dorsal margin long, straight, sloping, posterior margin narrowly rounded; ventral margin well rounded, concave at the flexure. Sculpture of numerous, small, radial spinose ribs, strongest at the posterior third, less so at the anterior third and almost obsolete at the medial third, more noticeable ventrally. Colour white, internally nacreous.

**MATERIAL EXAMINED.** HOLOTYPE: AMSC-120128, 1pv, NE of Lady Musgrave I., off central Qld, 23°38.8'S, 152°45.5'E, 365m, *Globigerina* mud and siliceous sponge, W.F. Ponder, I. Loch & P. Terrill, Dec 1977. Length 34.1mm, height 29.2mm, width 19.5mm. PARATYPES: AMSC321047, 2rv, same data as holotype. Length of largest rv 27.8mm, height 21.6, width rv 8.5mm; QMMO59367, 1pv, 1lv, Capricorn Channel, off central Qld, trawled, 128m. Length of pv, 42.3mm, height 35.3mm, width 24.8mm; length of lv, 38.1mm, height 32.0mm, width 11.7mm.

**HABITAT AND DISTRIBUTION.** Dredged in *Globigerina* mud and siliceous sand to 365m; central Qld

**REMARKS.** *Euciroa queenslandica* sp. nov. is similar in size to *E. galathea* (Dall, 1956). However *E. queenslandica* differs in having sloped anterior and posterior dorsal margins (almost straight in *E. galathea*) and being deeper in the posterior truncation, additionally it lacks the strong radial, medial sculpture of *E. galathea*. *E. queenslandica* differs from *Acreuciroa rostrata* Thiele & Jaeckel, 1931 in lacking the extended, narrowly attenuate posterior and the strong me-

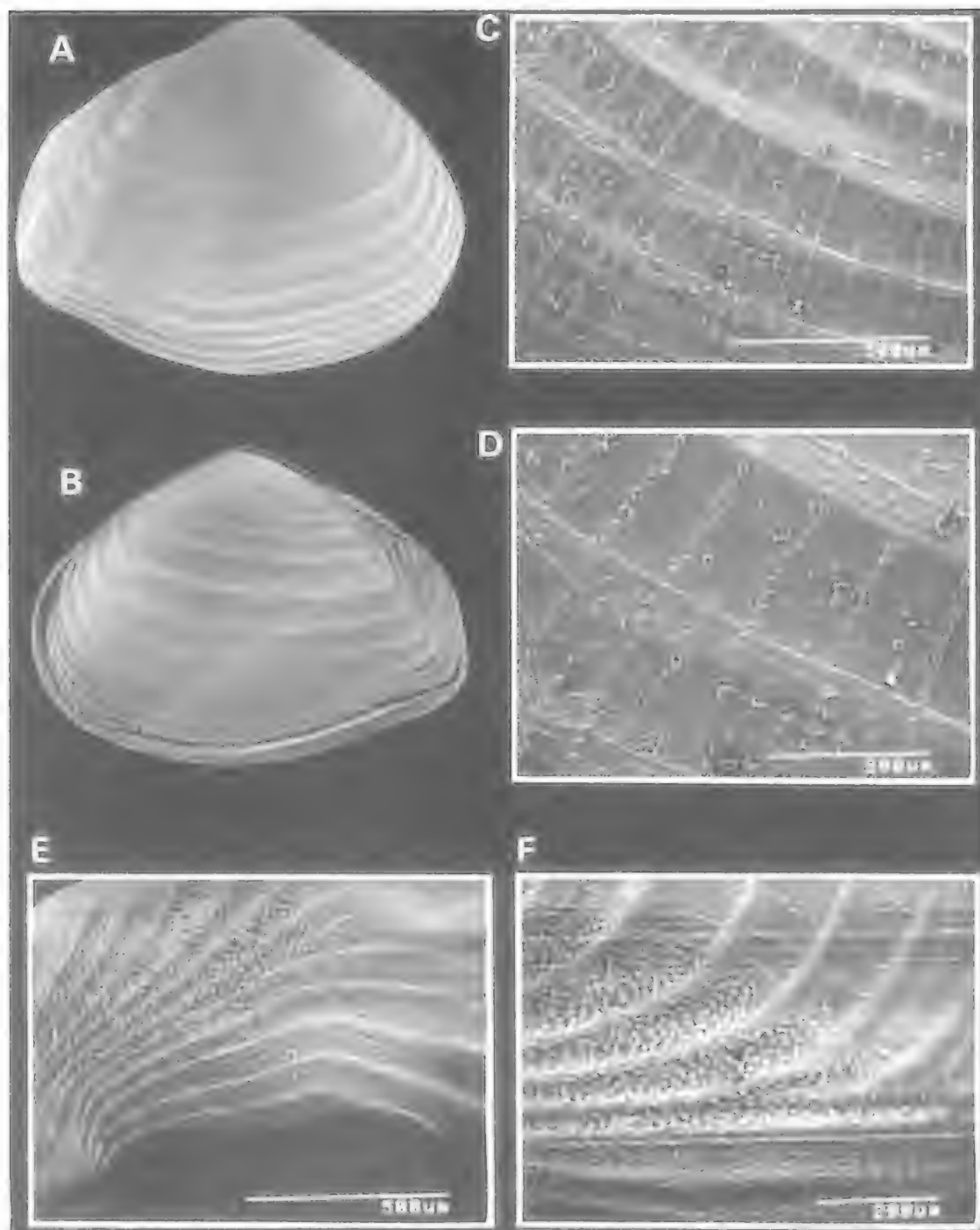


FIG. 4. A-F, *Corbula* (A.) *moretonensis* sp. nov. A, external view of rv; B, external view of lv; C, D, sculpture of rv showing radial pustules; E, F, sculpture showing concentric ridges and massed pustules of posterior margins.

dial radial sculpture of that species. *E. queenslandica* attains a far greater size than the Western Australian *E. granifera* (Cotton, 1931) and the Indo-Pacific (Northern Territory) *E. crassa* Thiele & Jaeckel, 1931, (42.3mm in *E. queenslandica*, 19.2mm in *E. crassa* and 6.8mm in *E. granifera*). *E. queenslandica* is more attenuate posteriorly than the Indo-Pacific *E. eburnea* Wood-Mason & Alcock, 1891 (roundly ovate in *E. eburnea*) while *E. eburnea* has denser radial sculpture. *E. queenslandica* lacks the transversely elongate shape of the large Indo-Pacific *E. trapezia* Poutiers, 1982 and has stronger radial sculpture posteriorly and ventrally.

Family CORBULIDAE Lamarck, 1818

*Corbula* Bruguière, 1797

TYPE SPECIES, *Corbula sulcata* Lamarck, 1801; SD-Schmidt, 1818

*Corbula* (Anisocorbula) Iredale, 1930

TYPE SPECIES, *Corbula macgillivrayi* Smith, 1885 - OD

*Corbula* (Anisocorbula) *moretonensis* sp. nov.  
(Fig. 4A-F)

ETYMOLOGY. For Moreton Bay.

DESCRIPTION. Shell length to 3.0mm, minute, solid, moderately inflated, inequivalve; rv more inflated, encompassing the slightly smaller lv, widely truncate, with a well-defined fold extending from the umbone to the posteroventral margin. Anterior margin steeply sloping, narrowly rounded terminally; posterior dorsal margin moderately sloping, angulate; ventral margin convex, concave anterior to the posterior ridge. Sculpture of strong, well-spaced, rounded, concentric ridges and wider interstices crossed by radial rows of minute pustules on both valves. Colour white.

MATERIAL EXAMINED. HOLOTYPE: QMMO-59365, 1pv, off Middle Banks, Moreton Bay, south-east Qld, W. Stephenson, between Sept 1972-June 1974. Length 3.0mm, height 2.2mm, width 1.7mm. PARATYPES: AMSC203162, 19pv, same data as holotype; AMSC203159, 17pv, same data as holotype; AMSC36301, many, Albany Passage, north Qld, 24m, C. Hedley.

HABITAT AND DISTRIBUTION. Dredged in sand to 10m; Moreton Bay, Qld.

REMARKS. Although *Corbula* (Anisocorbula) *moretonensis* sp. nov. is minute like *C.*

(*Notocorbula*) *monilis* Hinds, 1843 and *Corbula* (*Varicorbula*) *rotalis* Hinds, 1843. It can be readily separated from these species in having well defined, narrowly rounded, concentric ridges and wider interstices crossed uniquely by radial pustules on both valves while the sculpture in *C. (N.) monilis* consists of widely rounded concentric ridges, stronger at the ventral margin and obsolete at the umbones and without regular radial lines. *C. (V.) rotalis* has widely rounded concentric ribs on the rv while the lv is almost devoid of concentric sculpture but has well-defined radial ridges, absent on the rv. In addition the rv in *C. (A.) moretonensis* just moderately encompasses the lv while in *C. (N.) monilis* the rv is much larger than the lv, and in *C. (V.) rotalis* the lv is even smaller and more deeply encompassed. Very similar sculpture to that of *C. (A.) moretonensis* also occurs in *C. (A.) macgillivrayi* Smith, 1885 and *C. (A.) tahitensis* Lamarck, 1818, but these are much larger species (16-32mm) and more quadrate in shape than *C. (A.) moretonensis*.

*Corbula* (Notocorbula) Iredale, 1930

TYPE SPECIES, *Notocorbula vicaria* Iredale, 1930 - OD

*Corbula* (Notocorbula) *stephensoni* sp. nov.  
(Fig. 5A-E)

ETYMOLOGY. For the late William Stephenson.

DESCRIPTION. Shell length to 2.0mm, minute; moderately solid; inflated, inequivalve; rv inflated, widely truncate posteriorly; encompassing the much smaller lv. Anterior margin steeply sloping, widely rounded terminally; posterior dorsal margin long, moderately sloping; posterior margin angulate; ventral margin rounded, concave at the obscure ridge, umbones to posteroventral angle. Sculpture of rv medially with obscure concentric ridges, stronger ventrally with microscopic radial lirae; lv globose, smooth medially with obscure concentric striae stronger ventrally. Colour white.

MATERIAL EXAMINED. HOLOTYPE: QMMO-59366, 1pv, Cleveland Bay, north Qld, 19°15'S, 146°58'E, to 29m, Sept 1990. Length 2.0mm, height 1.54mm. PARATYPE: AMC203163, 1pv, same data as holotype.

HABITAT AND DISTRIBUTION. Dredged in sand to 29m; Cleveland Bay, north Qld.

REMARKS. *Corbula* (N.) *stephensoni* sp. nov. is similar to *C. (N.) monilis* Hinds, 1843, *C. (V.)*



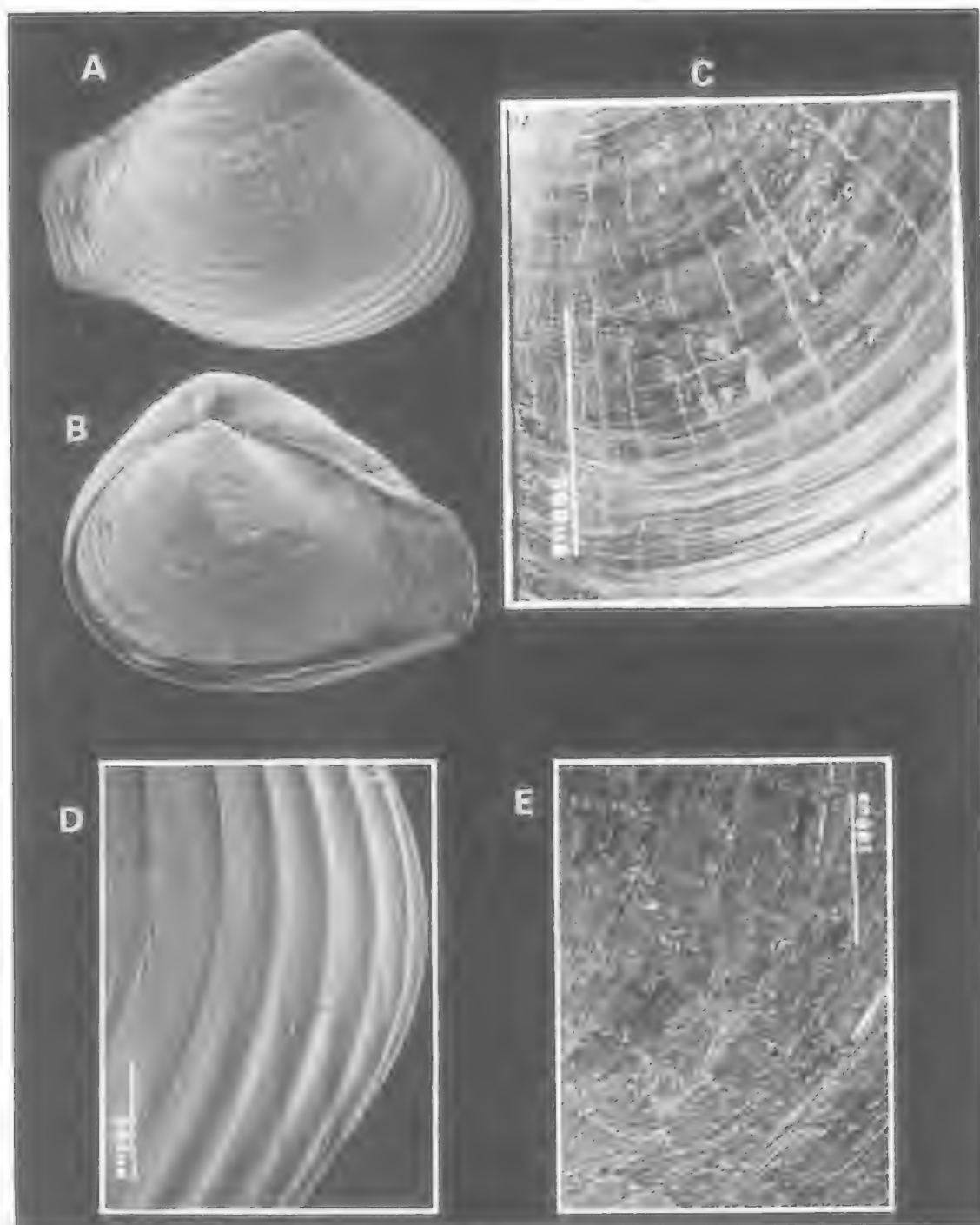


FIG. 5. A-E, *Corbula (N.) stephensoni* sp. nov. A, external view of rv; B, external view of lv; C, external view of rv sculpture; D, ventral sculpture in rv; E, posterior margin of lv showing detail of periostracal layers.



*rotalis* Hinds, 1843 and *C. (A.) moretonensis* in size. However *C. (V.) rotalis* and *C. (A.) moretonensis* have well-defined concentric sculpture with prominent interstitial radial lirae (both valves in *C. (A.) moretonensis*, lv in *C. (V.) rotalis*) while *C. (N.) stephensoni* has ventral concentric striae (obsolete medially) and microscopic radial lines on rv only. *C. (N.) stephensoni* is much more produced posteriorly than *C. (V.) monilis* and has a much narrower umbones (widely rounded in *C. (V.) monilis*).

#### ACKNOWLEDGEMENTS

We are grateful to Ms Kathy Way, Malacology Section of the British Museum (Natural History) for forwarding the type specimens of *Atrina (S.) penna* (Reeve) for this study; to Mr Ian Loch, Malacology Section, Australian Museum, Sydney for allowing access to the collection and providing loan material; and to Dr John Stanisic and reviewers for helpful criticism of the manuscript. Mr Philip Spoor assisted KL in dredging material of *A. (S.) palmensis* off Palm Is and Curacao Is during November 1990. Thanks are also due to Kylie Stumkat for the scanning electron micrographs of the corbulid specimens. Financial support for this project was provided by a Keith Sutherland Award to KL. An Australian Research Fellowship and Senior Research Fellowship from the Australian Research Council made possible the participation of JH.

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## ERRATUM

Gullan, P.J. & Stewart, A.C. 1996 07 20: A new genus and species of ant-associated coccid (Hemiptera: Coccidae: Myzolecaniinae) from *Canthium* Lam. (Rubiaceae). *Memoirs of the Queensland Museum* 39(2): 307-314. Brisbane. ISSN 0079-8835.

In the above paper the photograph on p. 307 was inadvertently printed upside down causing the caption to be misleading. Fig. 1 and its caption are reproduced correctly here.

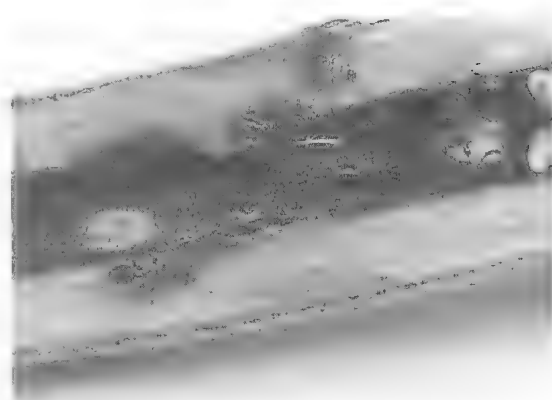


FIG. 1. Sectioned hollow stem of *Canthium odoratum* showing ant workers and larvae (*Podomyrma* sp.) on the right and an adult female of *Torarchus endocanthium* on the left.

PITAR RÖMER FROM AUSTRALIAN AND ADJACENT WATERS, WITH  
DESCRIPTIONS OF FOUR NEW SPECIES (MOLLUSCA: BIVALVIA: VENERIDAE)

KEVIN L. LAMPRELL AND JOHN M. HEALY

Lamprell, K.L. & Healy, J.M. 1997 06 30: *Pitar* Römer from Australian and adjacent waters, with descriptions of four new species (Mollusca: Bivalvia: Veneridae). *Memoirs of the Queensland Museum* 42(1): 283-306. Brisbane. ISSN 0079-8835.

Twenty seven species of *Pitar* (Veneroidea, Veneridae) occur in Australian waters. All are figured and described, including four new species, *P. (Hyphantosoma) caperi* sp. nov., *P. (Pitarina) queenslandica* sp. nov., *P. (P.) curnowae* sp. nov. and *P. (P.) thornleyae* sp. nov. and one new record *P. (H.) intricata* (Dautzenberg, 1907). *P. (H.) caperi* sp. nov. is also recorded from New Caledonian waters. *P. (Hyphantosoma)* is recorded from Australia for the first time, with five species assignable including three formerly included in *P. (Pitarina)* viz. *P. (H.) spoori* Lamprell & Whitehead, 1990, *P. (H.) nancyae* Lamprell & Whitehead, 1990 and *P. (H.) limatula* (Sowerby, 1853). □ Mollusca, Bivalvia, Veneridae, Australia, Pacific.

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*Pitar* Römer, 1857 occurs worldwide but is especially prolific and speciose in the Indo-West Pacific region and constitutes the largest group of venerids present in the Australian fauna. Although most species prefer shallow-water sandy-mud substrates, some occur among coral sand in reef lagoons or among shell debris in sandy mud to moderate depths (up to or occasionally exceeding 146 metres). Previous studies of Australian *Pitar* s.l. include Lamprell & Whitehead (1990), Healy & Lamprell (1992) and Lamprell & Stanisic (1996) resulting in a total fauna of 16 species. Harte (1993) recorded six fossil and five extant species in *Pitar (Hyphantosoma)*. She noted only one living species from the Western Pacific notably *P. (H.) intricata* (Dautzenberg, 1907) but four from the eastern Pacific — *P. (H.) aletes* Hertlein & Strong, 1948, *P. (H.) hertleini* Olsson, 1961, *P. (H.) pollicaris* (Carpenter, 1864) including one from Tahiti i.e. *P. (H.) festoui* Harte. Harte (1993) emphasized the presence of the fine zigzag sculpture in *Hyphantosoma* (absent in most other *Pitar*ines) which prompted a re-evaluation of the subgeneric assignments of the Australian *Pitar*. The present study demonstrates that in addition to *P. (H.) intricata*, Australia has four other species referable to *Hyphantosoma*, three of which were previously included in the subgenus *Pitarina* viz. *P. (H.) spoori* Lamprell & Whitehead, 1990, *P. (H.) nancyae* Lamprell & Whitehead, 1990 and *P. (H.) limatula* (Sowerby, 1853). Zigzag sculpture has also been observed in specimens of *P. (Pitarina) healyi* Lamprell & Stanisic, 1996 from New Cal-

edonia, suggesting perhaps that this species may be more correctly placed within the *P. (Hyphantosoma)* rather than *P. (Pitarina)*. However Harte (1993), while not dismissive of zigzag sculpture as an important feature of the subgenus *Hyphantosoma*, also raised the possibility that such sculpture could have been developed in more than one line of *Pitar*ines. In this account *Pitar* is reviewed and an additional five Australian species are described. The subgeneric status of all the species is reassessed in the light of Harte's (1993) review of *P. (Hyphantosoma)*. In addition, specimens of Australian species occurring in adjacent areas (Papua New Guinea, New Caledonia and Fiji) are recorded for the first time.

## MATERIALS AND METHODS

Material for this study derives from unsorted or part-sorted lots from the Queensland Museum, Brisbane (QMMO); Australian Museum, Sydney (AMSC); Museum of Victoria (MVF); Western Australian Museum (WAM); South Australian Museum (SAMD); Natural History Museum, London (BMNH); Museum national D'Histoire Naturelle, Paris (MNHN); National Science Museum, Tokyo (NSMT); and from the private collections of G. Curnow, Adelaide, South Australia; P. Spoor, Townsville, Queensland (PS) and one of the authors (KL).

Abbreviations used: lv = left valve; rv = right valve; pv = paired valves; AMS = Australian Museum, Sydney; GBR = Great Barrier Reef; KL = Lamprell Collection, Brisbane; MV = Museum

of Victoria; NEQ = northeastern Queensland; NSW = New South Wales; NT = Northern Territory; PNG = Papua New Guinea; Qld = Queensland; WA = Western Australia;

Shell height given is from the umbo to the ventral margin on the lv. Shell length given is the greatest distance from anterior to posterior margin. Shell width given is the greatest distance between the surfaces of the conjoined left and right valves. Shell size given is for the largest specimen examined by the authors unless otherwise stated.

Subgeneric divisions of *Pitar* as recognized by Keen (1969) in the *Treatise on Invertebrate Paleontology*, are used in the present study. All dimensions given in figure captions are shell length.

## SYSTEMATICS

Family VENERIDAE  
Subfamily PITARINAE

*Pitar* Römer, 1857

**DIAGNOSIS.** Shell ovate to subligonate and moderately inflated; umbones situated anteriorly; shell surface smooth or with obsolete concentric sculpture sometimes developed into zigzag patterns; lunule well defined; escutcheon obsolete.

*Pitar* (*Hyphantosoma*) Dall, 1902

**TYPE SPECIES** *Cytherea carbasea* Guppy, 1866, by original designation.

**DIAGNOSIS.** Sculpture of zigzag chiseled sculpture on at least part of the external surface of the shell.

*Pitar* (*Hyphantosoma*) *intricata*  
(Dautzenberg, 1907) (Fig. 1A,B; 8A)

*Meretrix* (*Pitar*) *intricata* Dautzenberg, 1907: 333, pl. 6, fig. 1; Harte, 1993: 347, fig. 3d,e; Lamprell & Stanisic, 1996: p. 47, fig. 6g,h.

**DIAGNOSIS.** Shell large, length to 53mm; solid, inflated. Sculpture of dense concentric ridges crossed by zigzag grooves, weaker medially. Colour light brown-white externally, internally white.

**MATERIAL EXAMINED.** HOLOTYPE: MNHN, label marked: Coll. types J. de Conch. V 1907 p.333 pl.VI f.1. OTHER MATERIAL. 1lv, AMSC142102, Samarang, Indonesia, 6°58'S, 110°25'E; 1rv, AMSC096751, Poindimié, New Caledonia, 20°56'S, 165°20'E; 1pv, MNHN, New Caledonia, Noumea, 9m;

1rv, AMSC156551, Port Mathurin, Rodrigues I, Mascarene Islands, 19°41'S, 63°25'E, mud and coralline dredgings; 1lv, AMSC123340, South I, Lizard I, GBR, 14°42'S, 145°27'E, outer side of reef; 1pv, PS, western side of Great Palm I, NEQ, 4m, in sand among coral; 1lv, AMSC306568, Cairns Reef lagoon, NEQ, 15°42'S, 142°30'E, 9-18m; 1lv, AMSC142103, Maculan I, Philippines, 10°5'N, 124°0'E, 7-30m, coral; 1rv, AMSC306573, Micronesia, Pohnpei, Caroline I, 6°55'N, 158°15'E, on rocks and broken coral, outer reef; 1lv, AMSC306668, Eel Reef, GBR, 12°24'S, 143°22'E, 4-8m; 1lv, 1rv, AMSC153285, No Name Reef, GBR, 14°40'S, 145°39'E, rubble at bommie base, Dec 1984.

**HABITAT AND DISTRIBUTION.** Among coral-sand in reef areas, to 18m; ranging from Mascarene Islands, Indonesia, Philippines, Caroline Islands, New Caledonia to northeastern Australia.

**REMARKS.** *P. (Hyphantosoma) intricata* (Dautzenberg, 1907) is easily recognised by its large size and fine zigzag sculpture. It is similar to *P. (H.) spoori* (Lamprell & Whitehead, 1990) in colour but larger, more inflated with stronger concentric sculpture and less quadrate posteriorly.

*Pitar* (*Hyphantosoma*) *spoori* Lamprell & Whitehead, 1990 (Fig. 1C-F; 8B)

*Pitar* (*Pitarina*) *spoori* Lamprell & Whitehead, 1990: 42, 3a-d; Lamprell & Whitehead, 1992: pl. 67, sp. 519; Lamprell & Stanisic, 1996: p. 44, fig. 5e-f.

**DIAGNOSIS.** Shell length to 35mm; quadrate, thin. Sculpture of dense concentric ridges crossed by zigzag grooves, weaker medially. Colour white, with sparse interrupted brown radial rays; wide brown radial ray covering posterior; escutcheon marked by a few, spaced brown lines; a deep brown spot often occurring beneath the umbones.

**MATERIAL EXAMINED.** HOLOTYPE: 1pv, AMSC133572, 3-6m, in gutters at top of drop off, N. West tip of reef, N of No.5 Bank Reef, NEQ, 13°40'S, 144°09'E. PARATYPES: AMSC142104, Broadhurst Reef, E of Townsville, NEQ, subtidal, 20 Jul 1975; 2lv, 2rv, QM1019860, Oipheus I, NEQ, subtidal, Jul 1985; 1lv, 2rv, AMSC155847, Michaelmas Cay, off Cairns, NEQ, GBR Boring Exp, May-Jun 1926; 1lv, 2rv, AMSC148161, Mystery Reef, Swain Reefs, NEQ, 4-6m around bommie in lagoon, 12 Jan 1985; 1pv, AMSC155850, Wheeler Reef, NEQ, subtidal; 2rv, AMSC155849, Lizard I, NEQ, 6-17m, in sandy rubble, 10 Dec 1974; 1lv, AMSC155848, Lizard I, NEQ, at base of reef, 9-12m, 11 Dec 1974. OTHER MATERIAL: 1lv, 1rv, AMSC153322, Reef 14-151, GBR, NEQ, 14°55'S, 145°41'E, 8-13m, among sand in coral heads, Dec 1984; 1lv, AMSC30666, Osprey Reef,

Coral Sea, 13°53'S, 146°31'E, 13-17m, Dec 1984; 1pv, AMSC30665, Reef 21-182, Swain Reefs, Qld, 21°22'S, 151°41'E, 10m, Jan 1995; 1pv, KL, Orpheus I, NEQ, in littoral sand near Octopus hole; 1pv, KL, Palm I side of Fantome I, low tide; 1rv, KL, Rudder Reef, NEQ, low tide.

**HABITAT AND DISTRIBUTION.** Among coral sand and rubble to 17m; ranging from Mascarene Islands, Mauritius, Indonesia, Philippines, Caroline Islands, New Caledonia, Papua New Guinea to northern Queensland.

**REMARKS.** *P. (Hyphantosoma) spoori* Lamprell & Whitehead, 1990 is quadrate posteriorly compared with *P. (Pitarina) pellucidus* (Lamarck, 1818) and *P. (P.) subpellucidus* (Sowerby, 1851) which are convex, thin and of similar size. *P. (H.) spoori* has a wide coloured posterior ray (no posterior radial ray in *P. (P.) pellucidus*), obscurely coloured on the median and anterior surface (strongly coloured in *P. (P.) subpellucidus*) and lacks the purple spots under the umbones that occur in *P. (P.) pellucidus*. Recent collecting in New Caledonia has produced the first known live-collected specimen of *P. (H.) spoori* (see Lamprell & Staniscic, 1996). Previously, this species was only known from dead shells taken in the littoral zone of northern Queensland (Lamprell & Whitehead, 1990).

***Pitar (Hyphantosoma) caperi* sp. nov.**  
(Fig. 1G,H; 8D)

**ETYMOLOGY.** For the vessel 'Caper'.

**DIAGNOSIS.** Shell length to 26.2mm quadrate, thin, inequilateral, anterior end of shell less than one third of maximum length, moderately inflated, light-weight; umbones oblique, approximate, lunule well defined, lanceolate, striate, surrounded by an impressed line; anterodorsal margin short, slightly convex, sloping, narrowly rounded terminally; posterodorsal margin slightly convex, gently sloping, broadly truncate posteriorly; ventral margin widely convex. Shell smooth with microscopic concentric ridges crossed anteriorly and posteriorly by obscure zigzag grooves; periostracum, thin, white, situated posteriorly and at the ventral margin. Ligament narrow, impressed. Hinge of lv with anterior lateral tooth long, peg-like; anterior cardinal thin, aeline, separated from median cardinal by inverted v-shaped socket; median cardinal solid, triangular; posterior cardinal free, thin, elongate and oblique; posterior lateral thin, parallel to nymph. Hinge of rv with peg-like anterior lateral

tooth; anterior and median cardinals peg-like, narrowly parallel, separate; posterior cardinal oblique, long, bifid; posterior lateral, parallel to nymph. Muscle attachment scars ill-defined, anterior adductor scar teardrop-shaped, posterior adductor scar large, somewhat ovate. Pallial line thin; pallial sinus extending approximately two-fifths towards the shell centre, wide, rounded terminally. Colour white, with interrupted tan-orange zigzag patterning over the whole surface; escutcheon and lunule crossed by tan lines; umbones with two broad, radial, well defined, white rays extending medially, internally white.

**MATERIAL EXAMINED.** HOLOTYPE: 1pv, AMSC202973, 6m, Little Upolo Cay, NEQ, P. Spoor, Oct 1983; length of shell 22.8mm, height 18.7mm, width of conjoined valves 11.7mm. PARATYPE: 1pv, MNHN, Anse Vata, Noumea, New Caledonia, 3m, Sep 1994; length of shell 26.2mm, height 20.2mm, width of conjoined valves 12.2mm. OTHER MATERIAL: 1pv, PS, same data as holotype; 1rv, N end of Fantome I, Palm Island Group, 1986; 1pv, KL, same data as paratype.

**HABITAT AND DISTRIBUTION.** Among coral sand to 6m; ranging from northeastern Queensland, Australia to New Caledonia.

**REMARKS.** *P. (Hyphantosoma) caperi* sp. nov. is similar to *P. (H.) spoori*, *P. (P.) pellucidus* (Lamarck, 1818) and *P. (P.) subpellucidus* (Sowerby, 1851) in shape but can be readily separated from these species by its zigzag sculpture on the external surface (concentric striae only on *P. (P.) pellucidus* and *P. (P.) subpellucidus*). *P. (H.) caperi* lacks the wide, brown, radial posterior ray and wider pallial sinus of *P. (H.) spoori*, while *P. (H.) spoori* lacks the two white radial rays of *P. (H.) caperi*. *P. (H.) caperi* appears to be a rare species. Examination of the extensive Australian Museum collection has failed to establish any further specimens other than those examined in this study.

***Pitar (Hyphantosoma) nancyae* Lamprell & Whitehead, 1990 (Fig. 11-L; 8F)**

*Pitar (Pitarina) nancyae* Lamprell & Whitehead, 1990: 45, 3c-h; Lamprell & Whitehead 1992: pl. 67, sp. 526; Lamprell & Staniscic, 1996: p. 45, fig. 6a,b.

**DIAGNOSIS.** Shell length to 36mm, moderately thin. Sculpture of microscopic concentric ridges crossed anteriorly and posteriorly by obscure zigzag grooves. Colour white, with wide, broken rays of brown; lunule and escutcheon sparsely marked with brown zigzag pattern; umbones pur-

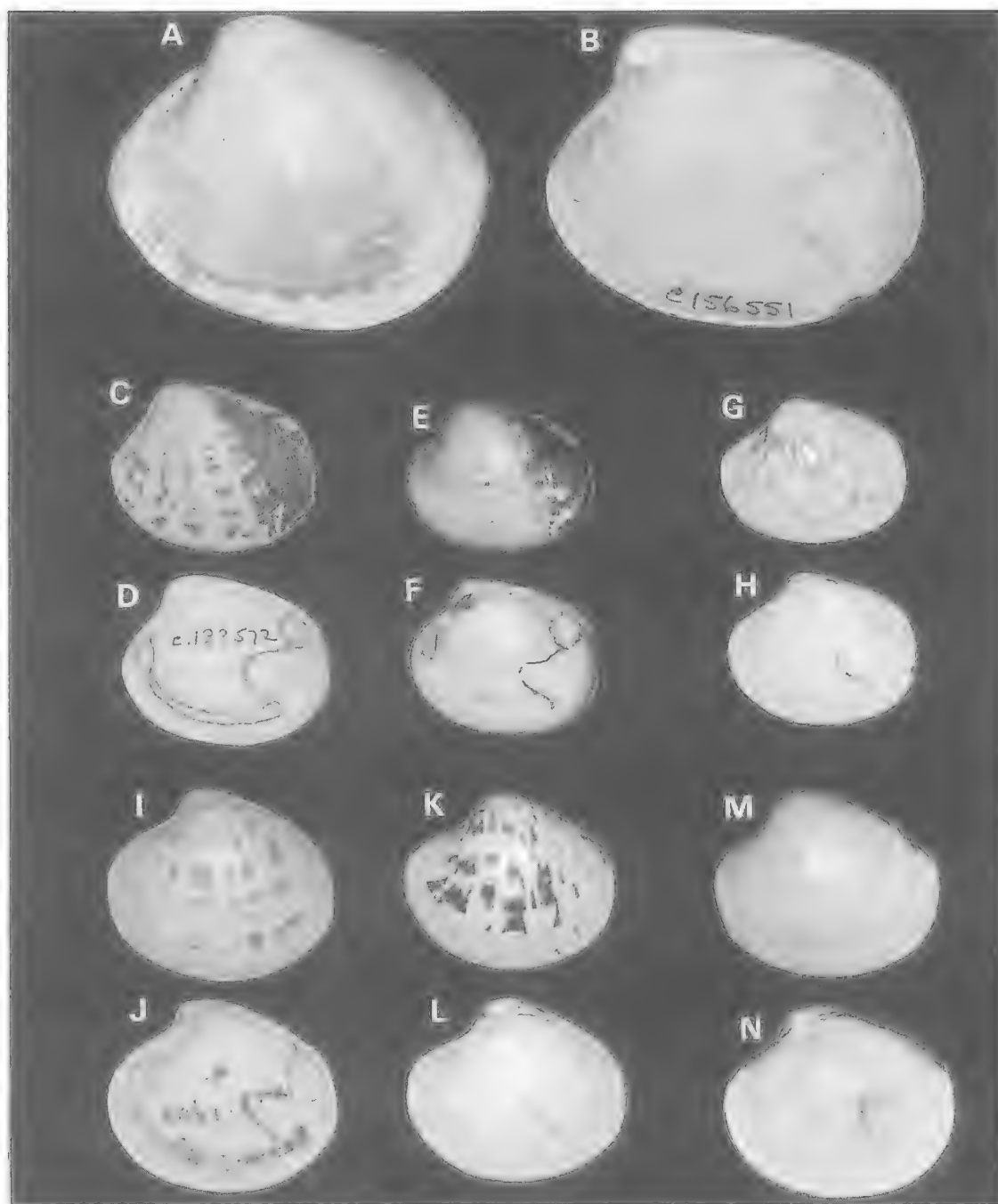


FIG. 1. A, B, *Pitar (Hypantostoma) intricata* (Dautzenberg). A, AMSC123340, Lizard Is, GBR, external lv (enlargement note zigzag sculpture on posterior third of valve), 52.7mm; B, AMSC156551, Mascarene Islands, internal rv (enlargement showing adductor scars and pallial sinus), 37mm. C-F, *P.(H.) spoori* Lamprell & Whitehead. C, D, holotype, AMSC133572, Bank Reef, NEQ, 31mm. C, external lv; D, internal rv. E, F, KL, Orpheus Is, 33mm. E, external lv; F, internal rv. G, H, *P.(H.) caperi* sp. nov., holotype, AMSC202973, Little Upolo Cay, NEQ, 22.8mm. G, external lv; H, internal rv. I-L, *P.(H.) nancyae* Lamprell & Whitehead; I, J, holotype, QMMO22851, Boyne Is, MEQ, 31mm. I, external lv; J, internal rv. K, L, KL, trawled Palm Is, NEQ, 28.8mm. K, external lv; L, internal rv. M, N, *P.(H.) limatula* (Sowerby), KL, Dingo Beach, central Qld, 24.2mm. M, external lv; N, internal rv.

ple tipped; interior white, with a small, intense purple spot inside the umbones.

**MATERIAL EXAMINED.** HOLOTYPE: 1pv, QMMO-22851, Boyne I, Qld, on beach near mouth of river, at low tide, Feb 1988. PARATYPES: 1pv, AMSC160472, same data as holotype; 1pv, AMSC160473, between Palm I and Curacoa I, NEQ, 10m, sand and rubble, 1pv, WAM940-89, between Palm I and Curacoa I, NEQ, 10m, sand and rubble; 1pv, MVF57680, Boyne I, Qld, in sand among shell debris after strong winds, on beach near mouth of river at low tide, Jan 1988. OTHER MATERIAL: 2rv, AMSC036338, off Murray I, Torres Strait, 9°56'S, 144°4'E, 9-15m, Aug 1907; 1lv, AMSC306543, Dunk I, Qld, 17°57'S, 146°10'E, Aug 1901; 2pv, 1lv, KL, Palm I, NEQ, trawled 10m, Aug 1994; 1pv, KL, Boyne I, Qld, beach, low tide, 1994; 8pv, 1lv, 2rv, KL, Palm I, trawled in Curacoa Channel to 10m; 1pv, KL, Rodds Bay, Turkey Beach, central Qld; 2pv, KL, off Caloundra, Qld, 79m.

**HABITAT AND DISTRIBUTION.** In sand and rubble to 79m; ranging from central Queensland to the Northern Territory, Australia and New Caledonia.

**REMARKS.** *P. (Hyphantosoma) nancyae* Lamprell & Whitehead, 1990 has previously been recorded only from the coasts of central to northern Queensland and New Caledonia. In Australia this species usually occurs in depths ranging from 9-30m, however the specimens collected from New Caledonia ranged from 33-60m. *P. (H.) nancyae* is similar to *P. (P.) sophiae* (Angas, 1877) but attains a much larger size and is more solid. This species has been included in *P. (Hyphantosoma)* on the basis of the zigzag sculpture on the anterior and posterior ends.

***Pitar (Hyphantosoma) limatula* (Sowerby, 1853) (Fig. 1M,N; 8C)**

*Cytherea limatula* Sowerby, 1853: 640, sp. 98, pl. 136, figs 200-201; *Pitar (Hyphantosoma) limatulum* (Sowerby) Habe, 1977: 257; *Pitar (Pitarina) limatula* Lamprell & Whitehead, 1992: pl. 67, sp. 525.

**DIAGNOSIS.** Shell length to 35mm; solid. Sculpture of fine concentric growth lines crossed by obscure zigzag grooves anteriorly and (rarely) posteriorly. Colour yellow, sometimes lightly flecked or rayed with chestnut-brown; escutcheon and lunule dark chestnut-brown.

**MATERIAL EXAMINED.** SYNTYPES: 2pv, BMNH1912.6.4.9-10, locality unknown; 1pv, AMSC306569, Wonga Beach, N of Mossman, NEQ, 16°22'S, 145°26'E, among rocks on sand and gravel;

5pv, 2rv, KL, Dingo Beach, central Qld, washed ashore after cyclone Aivu; 1pv, KL, Cape Upstart, NEQ, beach, 1987; 1pv, KL, Goold I, NEQ, low tide, Nov 1995.

**HABITAT AND DISTRIBUTION.** Among littoral sand and gravel; ranging from Japan to central and northern Queensland, Australia.

**REMARKS.** *P. (Hyphantosoma) limatula* (Sowerby, 1853) is readily distinguished from the other Australian *Pitar* species by the conspicuous dark staining on the lunule and escutcheon.

***Pitar (Pitarina) Jukes-Brown, 1913***

**TYPE SPECIES.** *Cytherea citrina* Lamarck, 1818 by original designation.

**DIAGNOSIS.** Posterior cardinal oblique, not attached to median cardinal; pallial sinus short. Sculpture of concentric sculpture only. (Diagnosis here emended).

***Pitar (Pitarina) citrina* (Lamarck, 1818) (Fig. 2A-C; 8E)**

*Cytherea citrina* Lamarck, 1818: 306; *Chione striata* Gray, 1838: 306; *Dione citrina* Reeve, 1863: pl. 10, fig. 43; *Dione usulata* Reeve, 1863: pl. 11, fig. 49. *Pitar (Pitarina) citrinus* Lamprell & Whitehead, 1992: pl. 67, sp. 520; *Pitar (Pitarina) citrina* Lamprell & Stanisic, 1996: p. 38, fig. 4c,d.

**DIAGNOSIS.** Shell length to 40mm; solid, inflated, subtrigonal to ovate. Sculpture of fine concentric lirae. Colour orange, yellow or sometimes white, with purple posteriorly; interior white with purple centrally and posteriorly.

**MATERIAL EXAMINED.** HOLOTYPE: Muséum de Genève, Lamarck collection, No. 24. OTHER MATERIAL. 7pv, KL, Shark Bay, northern WA, 1987; 4pv, KL, Back Beach, Dampier, northern WA, 1987; 2pv, KL, Broome, northern WA; MNHN, 3pv, Nouméa, New Caledonia; 4lv, MNHN, Platier Ouen Toro, New Caledonia; 2pv, MNHN, Presqu'île Nou Anse Kuenda, New Caledonia.

**HABITAT AND DISTRIBUTION.** In shallow, loose sand and eel grass; ranging from Japan (Habe, 1977 as *striata*) to north Western Australia, Northern Territory, Australia and New Caledonia.

**REMARKS.** *P. (Pitarina) citrina* (Lamarck, 1818) is a well known northern Western Australian species where it is found abundantly in loose sand and eel grass in shallow water. Typically it can be identified by its yellow external colour

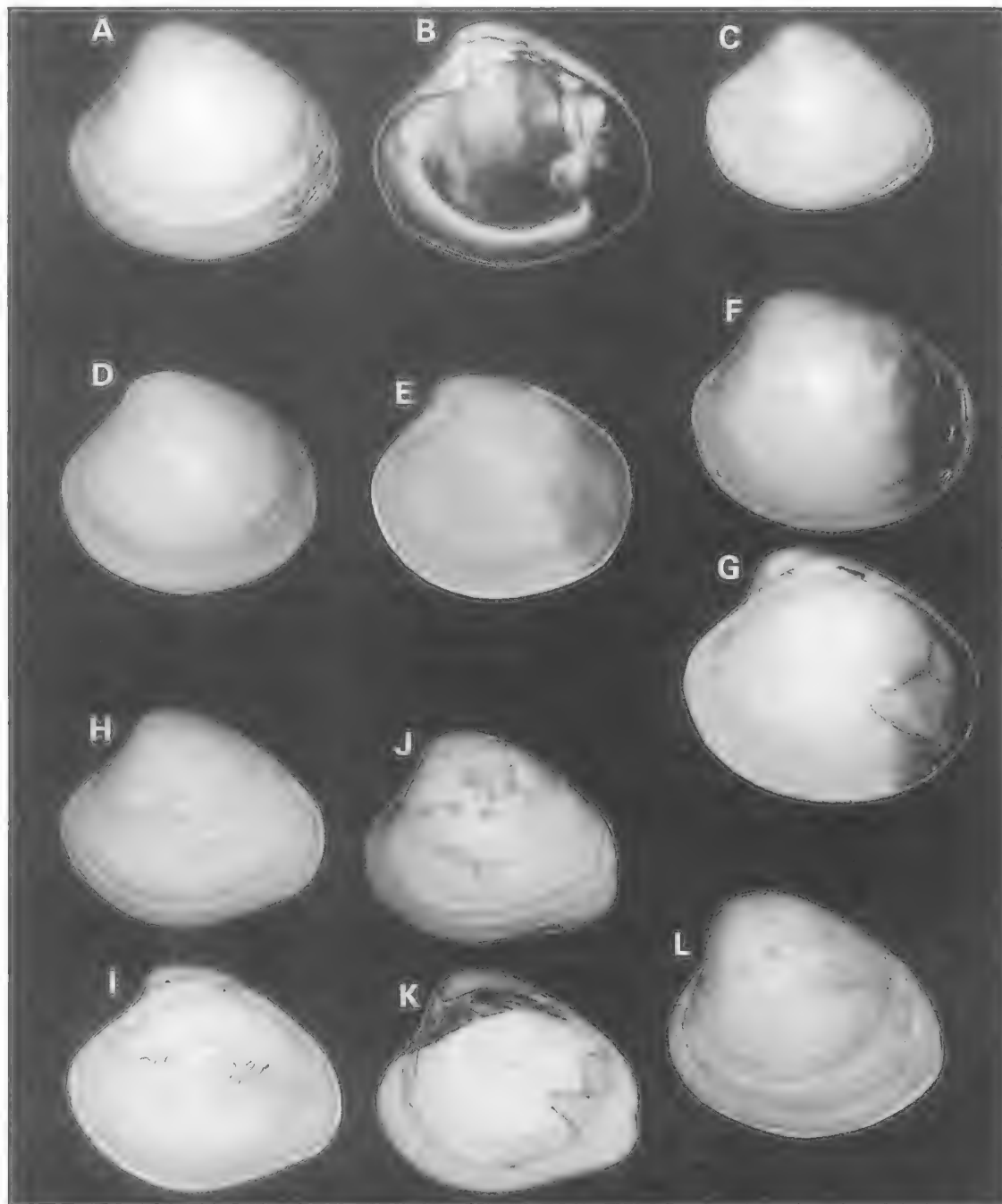


FIG. 2. A-C, *Pitar (Pitarina) citrina* (Lamarck). A, B, KL, Shark Bay, northern WA, 45.4mm. A, external lv; B, internal rv; C, KL, Broome, northern WA, external lv showing coloured rays, 38.5mm. D-G, *P.(P.) marrowae* Healy & Lamprell. D,E, holotype, QMMO32900, Dingo Beach, central Qld, 38.1mm. D, external lv; E, internal rv. F, G, KL, Goold Is, NEQ, 43mm. F, external lv; G, internal rv. H-L, *P.(P.) curnowae* sp. nov. H, I, holotype, AMSC202974, Madang, PNG, 42.7mm. H, external lv; I, internal rv. J, K, KL, Magnetic Is, NEQ. J, external lv; K, internal rv, 50mm (senile specimen). L, paratype, QMMO54081, Little Hope I, NEQ, external lv, 40mm.



(occasionally orange or white) and deep purple internal posterior. Specimens identifiable as *Chione striata* Gray, 1838 and *Dione ustulata* Reeve, 1863 occur sympatrically with *P. (P.) citrina* in northern Western Australia with intergrading shells which show without doubt that they are only forms of *P. (P.) citrina*.

**Pitar (Pitarina) marrowae** Healy & Lamprell, 1992 (Fig. 2D-G; 8J)

*Pitar (Pitarina) marrowae* Healy & Lamprell, 1992: 76; *Pitar (Pitarina) cf. osmunda* (Iredale, 1936) *sensu* Lamprell & Whitehead, 1992, pl. 67, sp. 521.

**DIAGNOSIS.** Shell length to 40mm; thin, inflated, subtrigonal to ovate. Sculpture of fine concentric lirae. Colour cream or fawn, with purple posteriorly; internally cream, with a purple stain at pallial sinus and posterior adductor scar.

**MATERIAL EXAMINED.** HOLOTYPE: 1pv, QMMO32900, on sandy mud flats at low tide, Dingo Beach, central Qld, 20°05'S, 148°30'E, 1985, KL. PARATYPES: 3pv, QMMO32901, Palm I, 18°40'S, 146°35'E, NEQ, subtidal, 1990; 3pv, AMSC166905, MVF60432, WAM559-91, Palm I, NEQ, 18°40'S, 146°35'E, subtidal, 1990, KL. OTHER MATERIAL: 3pv, KL, Palm I, NEQ, 18°40'S, 146°35'E, subtidal, 1990; 1pv, KL, Slashers Reef No. 1, GBR, 1993; 1pv, 1lv, KL, Goold I, NEQ, Nov 1955; 4lv, 1rv, AMSC306539, E of Moreton Bay, southern Qld, 26°54'S, 153°32'E, 115-176 m; 1rv, AMSC306541, Smith Point, Cobourg Peninsula, NT, 11°07'S, 132°08'E, Jun 1976.

**HABITAT AND DISTRIBUTION.** Buried in sand and rubble; ranging from New South Wales to northeastern Queensland, Australia, Papua New Guinea, Singapore, Bali, Samoa and the Philippines.

**REMARKS.** *P. (Pitarina) marrowae* Healy & Lamprell, 1992 differs from *P. (P.) citrina* (Lamarck, 1818) in being a much thinner shell, with a more convex posterior margin. This study has extends the known range to Papua New Guinea, Singapore, Bali, Philippines and Samoa.

**Pitar (Pitarina) curnowae** sp. nov.  
(Fig. 2H-L; 8H)

**ETYMOLOGY.** For Mrs G. Curnow.

**DESCRIPTION.** Shell subtrigonal, equivalve, inequilateral with the umbones situated at the anterior third, solid; umbones prosogyrate; lunule well developed, flat, striate, defined by a faint

impressed line; anterodorsal margin short, almost straight, steeply sloping, narrowly convex terminally; posterodorsal margin, long, slightly convex, steeply sloping, convex to truncate posteriorly; ventral margin convex anteriorly, sinuate posteriorly, more pronounced in mature specimens. Shell sculpture of strong, irregular concentric striae and irregular growth pauses. Periostracum, thick, grey, usually with agglutinated sand adhering to the posterior of the shell. Ligament, impressed, olive-brown in colour. Hinge of lv with anterior lateral tooth well developed, peg-like; anterior cardinal thin, joined to thick median cardinal forming an inverted v-shape; posterior cardinal long, ridge-like, free. Hinge of rv with pit for the reception of the lv lateral tooth; anterior cardinal short, narrow; median cardinal thick, straight; posterior cardinal well developed, bifid, oblique. Muscle attachment scars well defined; anterior adductor scar teardrop-shaped; posterior adductor scar larger and more round. Pallial sinus moderately short, ascending, rounded terminally. Shell colouration white or cream-white externally, escutcheon yellow-orange; internally white with yellow colour centrally extending to the posterior muscle scar.

**MATERIAL EXAMINED.** HOLOTYPE: 1PV, AMSC202974, purchased in market, Madang, PNG. Length of shell 42.7mm, height 35.3mm, width 26.1mm. PARATYPES: 1pv, SAMD18976, in littoral sand, Little Hope I, NEQ, 30 Jun 1988; 1pv, QMMO59380 in littoral sand, Little Hope I, NEQ, 30 Jun 1988; 4lv, 2rv, AMSC105230, 7pv, 2lv, 1rv, AMSC87941, Madang, PNG, 5°12.5'S, 145°47.5'E, swamp behind Nui I, among mangroves, 28 May 1970. OTHER MATERIAL: 1pv, KL, in littoral sand, Magnetic I, NEQ, O. Rippingale.

**HABITAT AND DISTRIBUTION.** In littoral sand and mangrove swamps; ranging from northern Queensland to Papua New Guinea.

**REMARKS.** *P. (Pitarina) curnowae* sp. nov is quite variable in shape. Younger specimens have an evenly convex ventral margin while senile specimens develop a concave (sinuate) ventral margin posteriorly and become more obese. *P. (P.) curnowae* is most similar to *P. (P.) citrina* (Lamarck, 1818) in having a similar solid, subtrigonal inequilateral shell but differing in having a sinuate margin posteriorly (evenly convex in *P. (P.) citrina*) and completely lacking any purple posterior colour. *P. (P.) curnowae* lacks the ovate shape of *P. (P.) affinis* (Gmelin, 1791) and the truncate posterior and anterior angulate margin of *P. (P.) prora* (Conrad, 1837) and does not attain

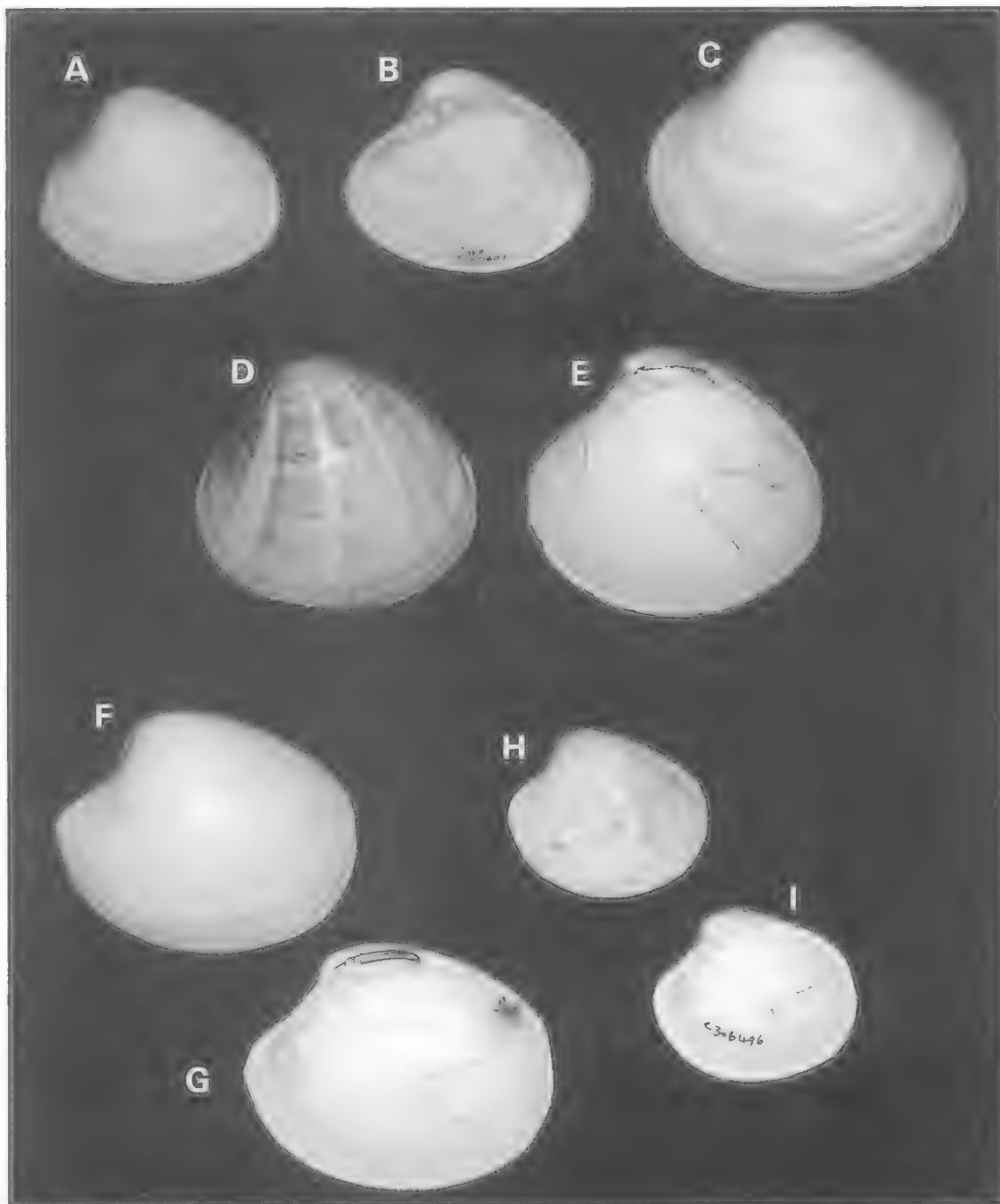


FIG. 3. A-C, *P. (Pitarina) osmunda* (Iredale), Sydney Harbour, NSW. A, AMSC320466, paralectotype, external lv, 39mm; B, AMSC60607, lectotype, internal rv, 38.5mm; C, AMSC303944, external lv, 36.5mm. D, E, *P. (P.) affinis* (Gmelin), KL, Shark Bay, northern WA, 56mm. D, external lv; E, internal rv. F-I, *P. (P.) prora* (Conrad); F, G, KL, North West I, 56.3mm. F, external lv; G, internal rv. H, I, AMSC306496, Mascarene Islands. H, external lv; I, internal rv, 37.2mm.

the large size of these species. *P. (P.) curnowae* lacks the wide convex posterior margin and light zigzag markings of *P. (P.) potteri* Healy & Lamprell, 1992 which is similar in size and valve inflation, but lacks a sinuate ventral margin. *P. (P.) curnowae* differs from *P. (P.) marrowae* in having a more solid shell and in lacking any purple colour posteriorly.

**Pitar (Pitarina) osmunda** (Iredale, 1936)  
(Fig. 3A-C; 8G)

*Pitarina osmunda* Iredale, 1936: 277.

**DIAGNOSIS.** Shell length to 39mm; solid, sub-trigonal. Sculpture of dense, fine concentric striae and irregular coarser growth lines. Colour dirty white internally and externally.

**MATERIAL EXAMINED.** LECTOTYPE: 1lv, AMSC60607, Sydney Harbour, NSW. PARALLECTOTYPE: 1lv, AMSC320466, same data as lectotype. OTHER MATERIAL: 1lv, AMSC303944, 'Triton Dredge', Sydney Harbour, NSW, 33°50'-33°52'S, 151°12'-151°16'E.

**HABITAT AND DISTRIBUTION.** Dredged in mud and littoral sand; known only from the type locality, Sydney Harbour, New South Wales

**REMARKS.** *P. (Pitarina) osmunda* (Iredale, 1936) is similar to *P. (P.) citrina* and *P. (P.) marrowae* in shape, but lacks the external yellow colour and purple internally and external posterior of both these species. *P. (P.) osmunda* is not as solid as *P. (P.) citrina* and has a more extended pallial sinus.

**Pitar (Pitarina) affinis** (Gmelin, 1791)  
(Fig. 3D,E; 9A)

*Venus affinis* Gmelin, 1791: 3278; *Pitar (Pitarina) affinis* (Gmelin) Prasad, 1932: 222; *Pitar (Pitarina) affine* Habe, 1977: 257; Lamprell & Whitehead 1992: pl. 67, sp. 514; Lamprell & Stanisic, 1996: p. 42, fig. 5a-b.

**DIAGNOSIS.** Shell length to 68mm, solid, glossy. Sculpture of fine concentric growth striae. Colour white or cream with tan-brown blotches and rays centrally and towards the umbones, purple spots sometimes occurring beneath umbones.

**MATERIAL EXAMINED.** 2pv, KL, Port Hedland, northern WA, in littoral sand, 1989; 1pv, KL, Monkey Mia, Shark Bay, northern WA, littoral sand, 1987; 1pv, KL, Capricorn Channel, central Qld, trawled; 4pv, KL, trawled Taylor Reef, NEQ, 10-12m, Dec 1995; 1pv, KL, Palm I, NEQ, 10m, Aug 1994; 5pv, KL, Curacao

Passage, Palm I, NEQ, Nov 1990; 1pv, KL, Dingo Beach, central Qld, in littoral sand; 1pv, KL, Fiji, on beach; 1pv, KL, PNG.

**HABITAT AND DISTRIBUTION.** In littoral sand and eel grass; ranging from Japan, Philippines, northeast and north Western Australia to New Caledonia.

**REMARKS.** *P. (Pitarina) affinis* (Gmelin, 1791) is the largest of the *P. (Pitarina)* species found in littoral sand. Examination of the shell middens on Stradbroke Island shows that the species was used as a major food source by the Aboriginal people of the island. *Cytherea inflata* Sowerby, 1851 appears to be a synonym of this well known species.

**Pitar (Pitarina) prora** (Conrad, 1837)  
(Fig. 3F-I; 8I)

*Venus prora* Conrad, 1837: 253; *Cytherea laeta* Lamarck, 1819: 307; *Cytherea obliquata* Hanley, 1844: 355 (app); *Pitar (Pitarina) obliquatum* (Hanley) Habe, 1977: 257; *Pitar (Pitarina) prora* (Conrad) Lamprell & Whitehead, 1992: pl. 66, sp. 513; Lamprell & Stanisic, 1996: 44, fig. 5c-d.

**DIAGNOSIS.** Shell length to 65mm; solid; lunule large. Sculpture of even, fine, concentric striae and growth lines. Colour usually white or cream, internally and externally; some specimens develop a fine tan zigzag or chevron pattern over the external surface.

**MATERIAL EXAMINED.** 1lv, AMSC306669, Port Mathurin, Rodrigues I, Mascarene Islands, 19°41'S, 63°25'E, mud and coralline dredgings; 1pv, 3rv, 2lv, AMSC306496, AMSC306497, Anse aux Anglais, Rodrigues I, Mascarene Islands, 19°43'S, 63°25'E, mud flats, May 1995; 1pv, AMSC306664, Mystery Reef, Swain Reefs, GBR, 21°23'S, 152°01'E, silt in lagoon, 10m, 13 Jan 1985; 1pv, KL, Feather Reef, NEQ, in lagoon; 1pv, KL, Suva, Fiji, in coral sand on reef; 1pv, KL, Apia, West Samoa, on reef flat; 1pv, KL, North West I, Bunker Group, in lagoon, 1991

**HABITAT AND DISTRIBUTION.** Among coral sand to 10m and on muddy sand flats at low tide; ranging from Arabia, Tanzania, Madagascar, Japan, Cocos-Keeling Islands, Hawaiian Islands, New Caledonia to the northeast coast of Australia.

**REMARKS.** *P. (Pitarina) prora* (Conrad, 1837) is the largest and heaviest shell in *P. (Pitarina)*. *P. (P.) prora* is not a common species throughout its range and is easily separated from other members of the genus by its almost pointed anterior

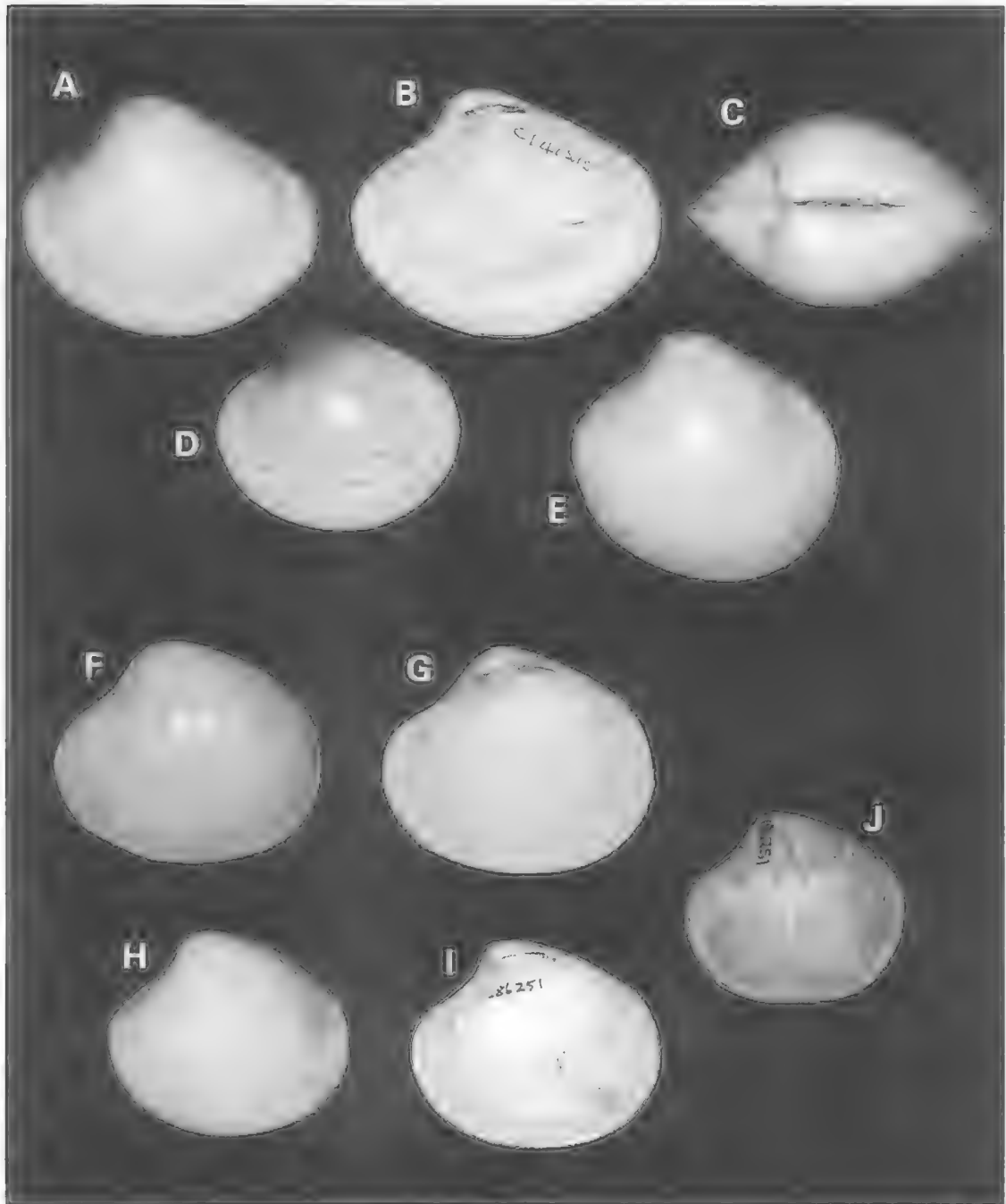


FIG. 4. A-E, *P. (Pitarina) pellucidus* (Lamarck). A-C, AMSC141215, Broome, WA, 34.4mm. A, external lv; B, internal rv; C, dorsal view of pv showing lunule and escutcheon. D, E, KL, Dingo Beach, central Qld. D, external lv, 33.7mm; E, external lv, 30.5mm. F-J, *P.(P.) potteri* Healy & Lamprell. F, G, holotype, QMMO32902, Palm Is, NEQ, 32.5mm; F, external lv; G, internal rv. H-J, AMSC086251, New Caledonia, 37.8mm. H, external lv; I, internal rv; J, external lv (length 34.5mm).

margin and subquadrate posterior. Specimens of *P. (P.) prora* have been examined from multiple lots which show obscure to strong tan radial patterns in some specimens while others have an all white surface. *Cytherea lactea* Lamarck, 1819 is lodged in the Museum de Genève (Collection Lamarck, No. 24, type lot 1084/27) and appears to be a synonym of this species, however the pallial sinus is deeper while another, smaller specimen from Lamarck's collection with the same registration number (1084/27) has a shallower pallial sinus similar to *P. (P.) prora*. Examination of the type of *Cytherea obliquata* Hanley, 1844: 355 (app) in the BMNH showed this to be conspecific with *P. (P.) prora*.

***Pitar (Pitarina) pellucidus* (Lamarck, 1818)**  
(Fig. 4A-E; 9B)

*Cytherea pellucida* Lamarck, 1818: 313; *Dione australica* Reeve, 1863: sp. 47, pl. 11; *Pitar (Pitarina) pellucidus* Lamprell & Whitehead, 1992: pl. 67, sp. 516; Lamprell & Stanisic, 1996: 42, fig. 4e-f.

**DIAGNOSIS.** Shell length to 45mm, thin, moderately inflated. Colour ranging from pure white to cream, usually with tan-coloured zigzag patterning, umbones often tinged light-brown with a purple spot beneath them.

**MATERIAL EXAMINED.** 1pv, BMNH1912.6.18.14, specimen figured by Sowerby (1853); 1pv, BMNH, holotype of *Cytherea australica* Reeve, 1863 from the Torres Strait. **OTHER MATERIAL:** 4rv, AMSC075783, Bathurst Head, Princess Charlotte Bay, NEQ, 14°16'S, 144°12'E; 1rv, AMSC142125, North Keppel I., Keppel Bay, central Qld, 23°04'S, 150°54'E, Aug 1946; 1pv, AMSC141215, Broome, WA, 17°58'S, 122°14'E; 2rv, 1lv, AMSC102766, Daintree River beach, NEQ, 16°17'S, 145°27'E, Nov 1928; 5pv, KL, trawled between Palfrey and Lizard Is, NEQ; 9pv, KL, Dingo Beach, central Qld, in littoral sand; 1pv, 1rv, KL, trawled to 10m, Little Trunk Reef, NEQ, Dec 1995; 5pv, KL, Suva, Fiji; 1pv, KL, Bundaberg, NEQ, littoral sand.

**HABITAT AND DISTRIBUTION.** Buried in shallow littoral sand; ranging from Japan, Philippines, New Caledonia, Solomon Islands, Fiji, Papua New Guinea, Australia from Queensland to northern Western Australia.

**REMARKS.** *P. (Pitarina) pellucidus* (Lamarck, 1818) is similar in shape to *P. (P.) subpellucidus* (Sowerby, 1851), *P. (P.) spoori* Lamprell & Whitehead, 1990 and *P. (P.) nancyae* but lacks the strong, broken radial rays of these species while the wide, shallow pallial sinus separates it from these and other Australian *Pitar* species.

***Pitar (Pitarina) potteri* Healy & Lamprell, 1992 (Fig. 4F-J; 9C)**

*Pitar (Pitarina)* sp. Lamprell & Whitehead 1992: pl. 67, sp. 515 (as *Pitar* sp.); *Pitar (Pitarina) potteri* Healy & Lamprell, 1992: 79; fig. 1e-h; Lamprell & Stanisic, 1996: 45, fig. 6c,f.

**DIAGNOSIS.** Shell length to 38mm, solid, inflated. Sculpture of microscopic concentric growth striae. Colour cream-white with faint tan zigzag patterns near umbones; interior white.

**MATERIAL EXAMINED. HOLOTYPE.** 1pv, QMMO32902, Palm I, NEQ, 18°40'S, 146°35'E, trawled in 9-12m in sand and rubble, Nov 1990. **PARATYPES:** 1pv, AMC142109, Broadhurst Reef east of Townsville, NEQ, 18°57'S, 147°47'E, subtidal 27-28 Sept. 1975; 1pv, AMSC105246, Watsons Bay, Lizard I, NEQ, 14°40'S, 145°27'E, 10.5m on sandy bottom, Dec 1975; 1pv, AMSC142108, Rudder Reef, NE Port Douglas, NEQ, 16°13'S, 145°40'E, intertidal, 1977; 1pv, AMSC08621, Lizard I, NEQ, 14°40'S, 145°28'E; 2pv, WAM560-91, MVF60433, Palm I, NEQ, 18°40'S, 146°35'E, subtidal, Nov 1990. **OTHER MATERIAL.** 4pv, 1rv, KL, dredged Taylor Reef, NEQ, 10m, coral sand, 1995; 1pv, KL, dredged in lagoon, Slashers Reef No. 1, GBR, Nov 1993; 4pv, 2rv, AMSC086261, Noumea, New Caledonia, 22°18'S, 166°29'E, among corals and rocks; 1rv, AMSC103582, Palfrey I., Lizard I, 14°41'S, 145°27'E, NEQ, in shell sand, 3 Dec 1974; 2rv, 1lv, AMSC041511, Lizard I, GBR, 14°40'S, 145°28'E, 18 Jul 1916; 1lv, AMSC126664, Eagle I, beach W side, Lizard I, GBR, 14°42'S, 145°23'E, 12 Dec 1974.

**HABITAT AND DISTRIBUTION.** Reef areas, in shell sand and rubble to 12m; ranging from northern Queensland to New Caledonia.

**REMARKS.** *P. (Pitarina) potteri* Lamprell & Whitehead, 1992 is similar to *P. (P.) affinis* (Gmelin, 1791) but does not attain the size of that species, is more inflated in proportion and has a more rounded and ascending pallial sinus.

***Pitar (Pitarina) trevori* Lamprell & Whitehead, 1990 (Fig. 5A-G; 9D)**

*Pitar (Pitarina) trevori* Lamprell & Whitehead, 1990: 47, 5a-d; Lamprell & Whitehead, 1992: pl. 67, sp. 517.

**DIAGNOSIS.** Shell length to 30mm; moderately inflated; lunule incised. Sculpture of fine concentric striae, periodically crowded as growth pauses. Colour all white; periostracum, pale straw coloured, usually with sand adhering to the external surface.

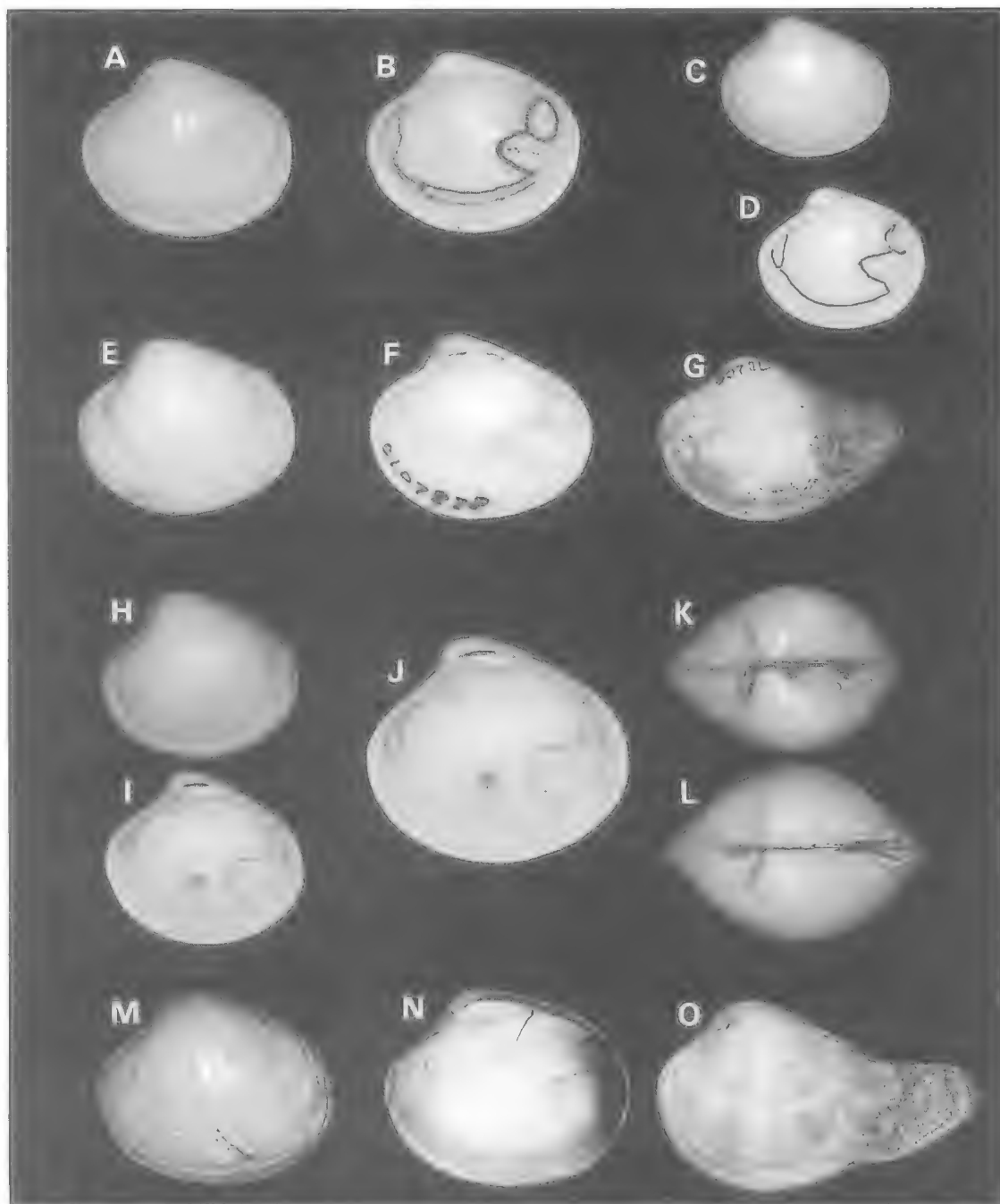


FIG. 5. A-G, *P. (Pitarina) trevori* Lamprell & Whitehead. A, B, holotype, QMMO22850, Dingo Beach, central Qld, 30mm. A, external lv; B, internal rv. C, D, KL, Turtle Is, Fiji, 30mm. C, external lv; D, internal rv. E, F, AMSC107878, Prince of Wales Is, north Qld, 29.3mm. E, external lv; F, internal rv. G, AMSC070200, Dingo Beach, central Qld, with siphon sheath attached, external pv, 31.3mm (including sheath). H-L, *P. (P.) queenslandica* sp. nov., holotype, AMSC306560, Black Is, NEQ, 21.1mm. H, external lv; I, internal rv; J, internal rv, enlargement; K, L, dorsal view of pv showing lunule and escutcheon. M-O, *P. (P.) subpellucidus* (Sowerby) KL, St Crispins Reef, NEQ, 33mm. M, external lv, N, internal rv; O, variation showing broad coloured rays, and with siphon sheath attached, external pv (length 43.9mm including sheath).

**MATERIAL EXAMINED.** HOLOTYPE: 1pv, QMM022850, on sand flats at low tide, Dingo Beach, central Qld, low tide, Jul 1987. PARATYPES: 1pv, MVF57679, same data as holotype; 1pv, AMSC160471, same data as holotype; 1pv, WAM939-89, on sand flats at low tide, Gove, NT, KL, Aug 1987. OTHER MATERIAL: 1pv, AMSC41611, Annan River near Cooktown, NEQ, Aug 1916; 1pv, 3rv, 1lv, AMSC107878, N of Terry Beach, W side of Prince of Wales I, Torres Strait, 10°42'S, 142°7'E, Jun-Jul 1976; 3rv, 2lv, AMSC306542, Lindeman I, central Qld, 20°27'S, 149°02'E, Nov 1934; 3rv, 2lv, AMSC306537, between Lindeman and Shaw Is, Kennedy Sound, central Qld, 20°25'S, 149°01'E; 2pv, AMSC070200, Cape Gloucester, Dingo Beach, 20°05'S, 148°30'E, central Qld; 4pv, KL, Kurrimine Beach, NEQ; 1pv, AMSC141215, Broome, northern WA, 17°58'S, 122°14'E; 2pv, KL, Turtle I, Fiji.

**HABITAT AND DISTRIBUTION.** Buried in shallow littoral sand; ranging in Australia from central Queensland to the Northern Territory, northern Western Australia to Fiji.

**REMARKS.** *Pitar* (*Pitarina*) *trevori* Lamprell & Whitehead, 1990 occurs sympatrically with *P. (P.) pellucidus* (Lamarck, 1818) but that species differs in being more inflated, having an incised lunule and completely lacking the umbonal colouring and umbonal spot of that species.

***Pitar* (*Pitarina*) *queenslandica* sp. nov.**  
(Fig. 5H-L; 9E)

**ETYMOLOGY.** For Queensland.

**DESCRIPTION.** Shell length to 22.3mm, sub-trigonal, equivalve, inequilateral (the umbones situated forward of centre), thin; umbones prosogyrate; lunule well developed, heart-shaped, striate, raised centrally, defined by a faint impressed line; anterodorsal margin short, almost straight, steeply sloping, convex terminally; posterodorsal margin, long, slightly convex, steeply sloping, convex to slightly truncate posteriorly; ventral margin evenly convex. Shell sculpture of well defined concentric striae, obsolete umbonally, stronger marginally. Periostracum, thick, grey with agglutinated sand adhering to the shell margins. Ligament, impressed. Hinge of lv with anterior lateral tooth well developed, peg-like; anterior cardinal thin, joined to thick median cardinal forming an inverted v-shape; posterior cardinal long, thin, ridge-like, free. Hinge of rv with hinge line expanded ventrally at pit for the reception of the lv lateral tooth; anterior cardinal, narrow; median cardinal free, slightly oblique; posterior cardinal bilid, oblique. Muscle

attachment scars well defined; anterior adductor scar teardrop-shaped, posterior adductor scar larger and more rounded. Pallial sinus extends medially, one third of the shell length, moderately wide, rounded terminally. Shell colour internally and externally glossy white.

**MATERIAL EXAMINED.** HOLOTYPE: 1pv, AMSC306560, Black I, Langford Reef, central Qld, 20°05'S, 148°54'E, dredged, 18m, Nov 1969. Length of shell 21.1mm, height 18.4mm, width 13.65mm. PARATYPES: 4pv, 2lv, 1rv, AMSC96704, dredged off Lindeman I, central Qld, 1935; 2lv, 6rv, AMSC306534, SE of Sarina, central Qld, 21°47'S, 150°34'E, dredged 59m, Dec 1977; AMSC58758 (pt), dredged off Lindeman I, central Qld, Aug 1935; 1pv, QMM059380, Gulf of Carpentaria, 12°22'S, 141°35.2'E, 13m. OTHER MATERIAL: 1rv, AMSC306556, off Caloundra, southern Qld, 26°47'S, 153°35'E, 128m, Mar 1969; 3lv, 2rv, AMSC58758 (pt), off Lindeman I, central Qld, Aug 1935; AMSC306533, E of Sarina, central Qld, 21°28'S, 150°08.5'E, sandy mud, Nov 1977; 1lv, AMSC306557, Caloundra, southern Qld, 26°49'S, 153°09'E, beach, Oct 1963; 2lv, 4rv, AMSC306562, Caloundra, southern Qld, 26°49'S, 153°10'E, beach; 9lv, 6rv, AMSC306540, E of Broad Sound, southern Qld, 21°58.5'S, 150°45'E, 57m, in coarse to fine sand and mud, Nov 1977; many juveniles, AMSC029671, Cairns Reef, NEQ, 15°42'S, 142°30'E, 9-18m, Aug 1906; 2rv, 1lv, AMSC306559, off Cairns, NEQ, 16°51.6'S, 146°1.2'E, 33-35m, sandy-mud and shell, Oct 1981; 2lv, 1rv, AMSC306532, E of Mackay, central Qld, 20°52'S, 149°29'E, 35m 1977; 1pv, AMSC093523, Point Cartwright, southern Qld, 26°41'S, 153°08'E, 1963; 4pv, 1pv, KL, Llewellyn Bay, Armstrong Beach, Sarina, central Qld, after storm, Apr 1995; KL, Gulf of Carpentaria, NEQ, 11°10.2'S, 139°03.2'E, 52.5m.

**HABITAT AND DISTRIBUTION.** Dredged in silty sand to 128m; appears to be restricted to Queensland.

**REMARKS.** *P. (Pitarina)* *queenslandica* sp. nov. is a small species, the largest specimen sighted, AMSC306556 is 22.3mm. It is most like *P. (P.) trevori* Healy & Lamprell, 1992 which is also glossy white with a subtrigonal shell. However *P. (P.) queenslandica* is readily separated by its much smaller size, ventrally expanded hinge line (straight in *P. (P.) trevori*) and much deeper pallial sinus. Compared with *P. (P.) pellucidus* (Lamarck, 1818), *P. (P.) subpellucidus* (Sowerby, 1851), *P. (P.) lineolatus* (Sowerby, 1854) and *P. (Hyphantesoma)* *limatula* (Sowerby, 1853), *P. (P.) queenslandica* does not attain the size of these species, has a more extended pallial sinus and does not exhibit a colour pattern (uniformly



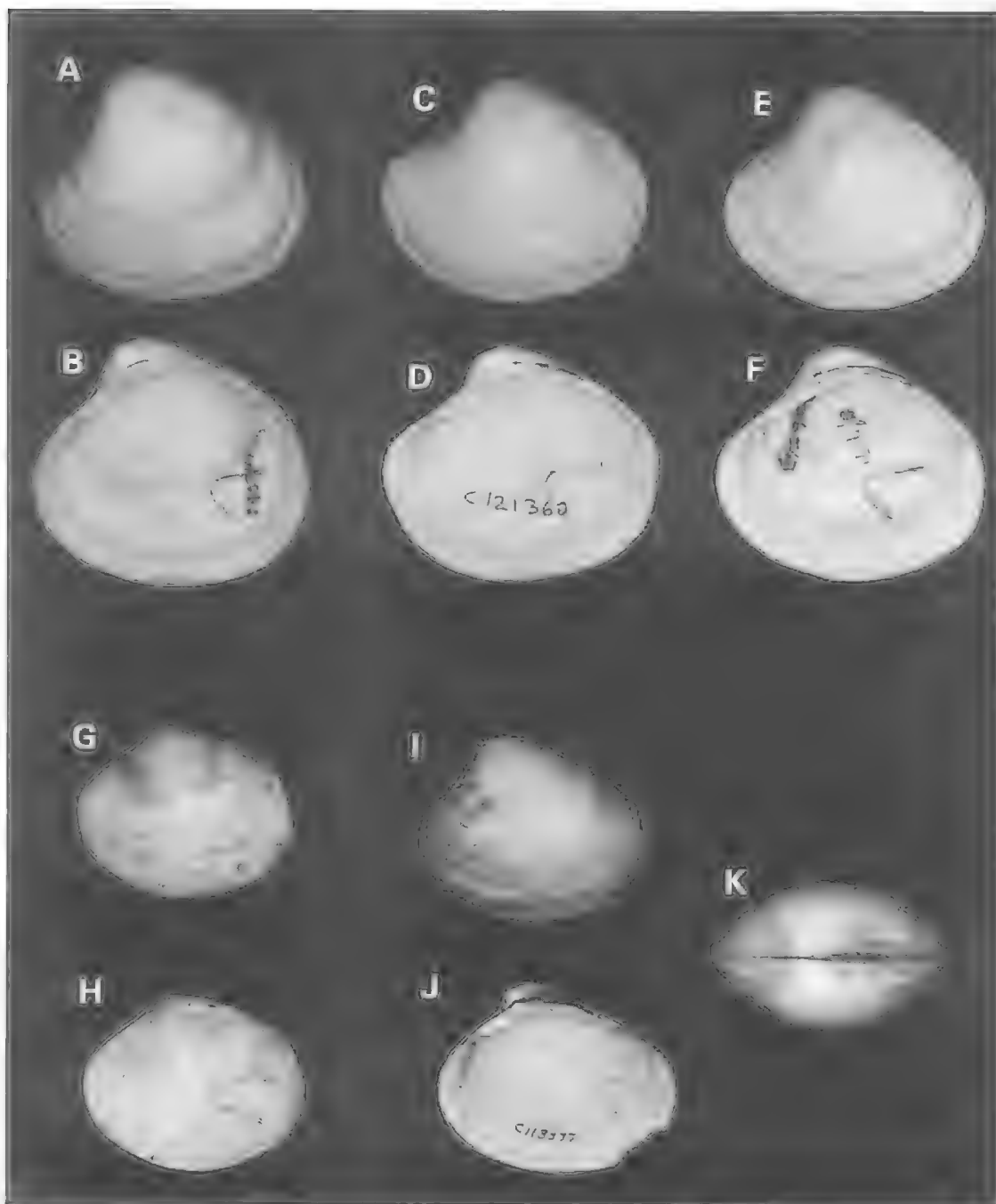


FIG. 6. A, B, *P. (Pitarina) japonicus* Kuroda & Kawamoto, AMSC095267, south of Yeppoon, Qld, 37.6mm. A, external lv; B, internal rv. C, D, *P. (P.) noguchii* Habe, AMSC121360, Roebuck Bay, Broome, northern WA, 37.3mm. C, external lv; D, internal rv. E, F, *P. (P.) nipponica* Kuroda & Habe, AMSC306563, Shelley Beach, Townsville, north Qld, 27.3mm. E, external lv; F, internal rv. G, H, *P. (P.) sophiae* (Angas), KL, off Caloundra, Qld, 28.9mm. G, external lv; H, internal rv. I-K, *P. (P.) thornleyae* sp. nov., holotype, AMSC113277, Karumba, Gulf of Carpentaria, north Qld, 46.8mm. I, external lv; J, internal rv (broken ventro-posterior margin); K, dorsal view pv showing lunule and escutcheon.



glossy white in *P. (P.) queenslandica*). Compared with *P. (P.) coxeni* (Smith, 1885) and *P. (P.) sophiae* (Angas, 1877) which are also small in size and approximately similar in shape, *P. (P.) queenslandica* does not have the colour pattern usually evident in *P. (P.) sophiae* while the pallial sinus is deeper in *P. (P.) queenslandica* than in both *P. (P.) sophiae* and *P. (P.) coxeni* (sinus angulate in *P. (P.) coxeni*).

***Pitar (Pitarina) subpellucidus***  
(Sowerby, 1851) (Fig. 5M-O; 9F)

*Cytherea subpellucidus* Sowerby, 1851: 639, pl. 133, f. 136; *Diene torresica* Reeve, 1863: pl. 11, sp. 51; *Pitar (Pitarina) subpellucidus* (Sowerby) Habe, 1977: 257; Lamprell & Whitehead, 1992: pl. 67, sp. 517.

**DIAGNOSIS.** Shell length to 40mm, elongate ovate, moderately inflated. Sculpture of fine concentric striae. Colour cream with dense brown radial rays, purple posteriorly; umbones brown with purple spots beneath; interior tinged purple posteriorly.

**MATERIAL EXAMINED.** KL, 1pv, Barber I, NE Palm I, NEQ; KL, 1pv, St Crispins Reef, NEQ; KL, 1pv, Low I, NEQ; KL, 1pv, Cobham Reef, near Gould Reef, central Qld; KL, 1pv, Palm I, NEQ, dredged to 10m; KL, 4pv, Lizard I, between Palfrey and Eagle I, NEQ, 29m.

**HABITAT AND DISTRIBUTION.** Dredged to 10m in coral and littoral sand, coastal and GBR; ranging from Japan to Queensland, Australia.

**REMARKS.** This is not a common species but appears to be widely distributed, further collecting should increase the known range of the species. *P. (P.) subpellucidus* (Sowerby, 1851) is similar in shape to *P. (P.) pellucidus* (Lamarck, 1818) but is readily distinguished by its more highly coloured shell.

***Pitar (Pitarina) japonicus* Kuroda & Kawamoto, 1956** (Fig. 6A,B; 9G)

*Pitar (Agriopoma) japonicum* Kuroda & Kawamoto, 1956: 89, figs 1-4; *Pitar (Pitarina) japonicum* Habe, 1977: 257; Lamprell & Whitehead 1992: pl. 67, sp. 522; Lamprell & Staniscic, 1996: 44, fig. 5g,h.

**DIAGNOSIS.** Shell length to 35mm; thin, ovate-trigonal, umbones prosogyrous. Sculpture of fine concentric growth lines. Colour cream-white, with pale orange or pink umbones and interior.

**MATERIAL EXAMINED.** 2pv, AMSC106921, South Great Keppel I, central Qld, 23°12'S, 150°58'E; 2rv, 2lv, AMSC093524, Keppel Bay, central Qld, 23°25'S, 150°55'E; 1pv, AMSC095267, Zilzie Point, central Qld, 23°17'S, 150°50'E, sheltered mud flats; 1pv, KL, Lammermoor Beach, central Qld, after storm; 1pv, KL, Boyne Is Beach, central Qld, low tide; 1pv, KL, Dingo Beach, central Qld, low tide; 1rv, AMSC142126, Penguin Channel, GBR, 16°15'S, 145°31'E, 18-28.5m; 1pv, 1rv, KL, Shelburne Bay, NEQ, 12°41'3'S, 140°42.5'E, Jan 1993; 1pv, AMSC092622, Groote Eylandt, Gulf of Carpentaria, 14°00'S, 136°25'E, Oct. 1973; 1rv, AMSC306565, 32km off Point Charles, Darwin, NT, 12°10'S, 130°22'E, 237m, Jul 1938.

**HABITAT AND DISTRIBUTION.** Buried in tidal sand and mud; ranging from Japan, New Caledonia, central Queensland to northern Australia.

**REMARKS.** *P. (Pitarina) japonicus* Kuroda & Kawamoto, 1956 is reasonably common throughout its range. Recent records from New Caledonia mark the southern limit of its distribution.

***Pitar (Pitarina) noguchii***  
Habe, 1958 (Fig. 6C,D; 9H)

*Pitar (Agriopoma) noguchii* Habe, 1958: 34; *Pitar (Pitarina) noguchii* Habe, 1964: pl. 58, fig. 6; Habe, 1977: 257; Lamprell & Staniscic, 1996: 42, fig. 4g-h.

**DIAGNOSIS.** Shell length to 37.3mm, thin, inflated. Sculpture of fine concentric ridges and irregular blue growth pauses, with small puncture marks over surface. Colour white internally and externally.

**MATERIAL EXAMINED.** 1pv, AMSC121360, Roebuck Bay, Broome, northern WA, 18°00'S, 122°15'E; 1pv, AMSC13871, North Keppel Island, Keppel Bay, central Qld, 23°04'S, 150°54'S, 1970; 1pv, AMSC308648, Philippines, purchased from Sowerby and Fulton, presented by C. Hedley.

**HABITAT AND DISTRIBUTION.** Dredged in sand to 150m; ranging from Japan to New Caledonia and Australia from Queensland to north Western Australia.

**REMARKS.** Hitherto only recorded from Japan, recent collecting has extended the known distribution to New Caledonia (Lamprell & Staniscic, 1996). These appear to be the first records of the species from Australia which is a significant range extension.

**Pitar (Pitarina) nipponica** Kuroda & Habe,  
1971 (Fig. 6 E,F; 91)

*Pitar (Pitarina) nipponica* Kuroda & Habe, 1971;  
Habe, 1977: 257; Lamprell & Whitehead, 1992: pl.  
67, sp. 531.

**DIAGNOSIS.** Shell length to 23mm; subtrigonal. Sculpture of fine concentric growth striae; surface covered with small, random puncture marks. Colour white, externally; interior white, yellow centrally.

**MATERIAL EXAMINED.** HOLOTYPE: 1pv, NSMT, MOR9601, Amadai-ba [bank], off Hayama, Sagami Bay, [Kanagawa, Japan] 1971. OTHER MATERIAL: 3lv, AMSC093520, South West Rocks, Trial Bay, central NSW, 30°53'S, 153°04'E, beach, Aug 1960; 1pv, AMSC306545, off Tweed Heads, north-eastern NSW, 28°08'-28°12'S, 153°40'-153°45'E, 54m, Oct 1936; 4rv, 2lv, AMSC054657, Caloundra beach, southeastern Qld, 26°49'S, 153°10'E, May 1926; 1pv, KL, Pallarenda Beach, Townsville, NEQ, low tide; 3pv, KL, AMSC306563, AMSC142127, Shelley Beach, Townsville, NEQ, 19°11'S, 146°45'E, low tide, Aug 1970; 1pv, KL, Exmouth Gulf, WA; 1pv, KL, Arafura Sea, Bureau of Rural Resources, 1990.

**HABITAT AND DISTRIBUTION.** Buried in littoral sand and to 54m; ranging from Japan to Queensland and north Western Australia.

**REMARKS.** *P. (Pitarina) nipponica* Kuroda & Habe, 1971 is similar to *P. (P.) japonicum* Kuroda & Kawamoto, 1956 but is smaller, has more lightly coloured umbones and random puncture marks on the external surface.

**Pitar (Pitarina) sophiae** (Angas, 1877)  
(Fig. 6G-H; 10A)

*Cytherea sophiae* Angas, 1877: 176, pl.26, f.23; *Pitar (Pitarina) sophiae* (Angas) Lamprell & Whitehead, 1992: pl. 68, sp. 531; Lamprell & Stanisic, 1996: 45, fig. 6c-d.

**DIAGNOSIS.** Shell length to 17mm, thin, inflated. Sculpture of concentric growth striae, surface smooth, glossy. Colour white, with grey concentric bands, sometimes with faint brown broken rays; umbones usually tinged with red anteriorly, visible internally.

**MATERIAL EXAMINED.** 2rv, AMSC306495, Manly Beach, Sydney, NSW, 33°48'S, 151°17'E; 1pv, AMSC306544, ENE of Point Danger, northern NSW, 27°04'-27°59'S, 153°50'E, 137-146m; 1pv, AMSC007545, inner North Head, Port Jackson, Sydney, NSW, 33°49'S, 151°17'E, 15m, in sand; 1rv,

AMSC306571, Christmas I, off NE point, 10°25'S, 105°42'E, 183m.

**HABITAT AND DISTRIBUTION.** Dredged to 183m in sand; ranging from New South Wales, central to northern Queensland, Australia, Christmas I, to New Caledonia.

**REMARKS.** Smith (1885) considered *P. (Pitarina) sophiae* (Angas, 1877) to be a synonym of *Cytherea hebraea* Lamarck, 1818. However comparison of specimens of *P. (P.) sophiae* in the Australian Museum and the holotype of *P. (P.) hebraea* in the Museum de Geneve shows that *P. (P.) sophiae* is longer in proportion to height than *P. (P.) hebraea*, is more widely rounded at the anterior and posterior margins, does not attain the size of that species and has a pink flush on the inner side of the valves of many specimens. Additionally, the pallial sinus in *P. (P.) hebraea* is wider, deeper and less ascending than in *P. (P.) sophiae*.

**Pitar (Pitarina) thornleyae** sp. nov.  
(Fig. 6I-K; 10B)

**ETYMOLOGY.** For Ms Gertie Thornley.

**DIAGNOSIS.** Shell length to 46.8mm, elongate ovate, equivalve, inequilateral, the anterior end of shell being 1/3 of the shell length; moderately inflated, thin; umbones approximate, lunule narrowly heart-shaped, striated, surrounded by an impressed line; anterodorsal margin moderately convex, sharply sloping, narrowly rounded terminally; posterodorsal margin almost straight, gently sloping, posterior margin narrowly rounded; ventral margin convex. Sculpture of coarse, irregular concentric ridges and growth pauses; periostracum grey, with sand adhering to most of shell surface. Ligament, narrow, partially external. Hinge of lv with anterior lateral tooth narrow, peg-like, moderately thick; anterior cardinal, slightly oblique; median cardinal solid, broad, raised; posterior cardinal long, oblique; posterior lateral, long, thin, parallel to the nymph. Hinge of rv with paired anterior laterals, separated by a deep pit; anterior cardinal thin, raised; median cardinal thin, not joined, parallel to anterior cardinal, separated by a narrow pit; posterior cardinal oblique and bifid; posterior lateral long, solid, parallel to the nymph. Muscle adductor scars well defined, anterior adductor scar elongate-ovate, posterior adductor scar teardrop-shaped. Pallial line ragged. Pallial sinus extending one third medially, triangular. Colouration off-white externally, internally white.

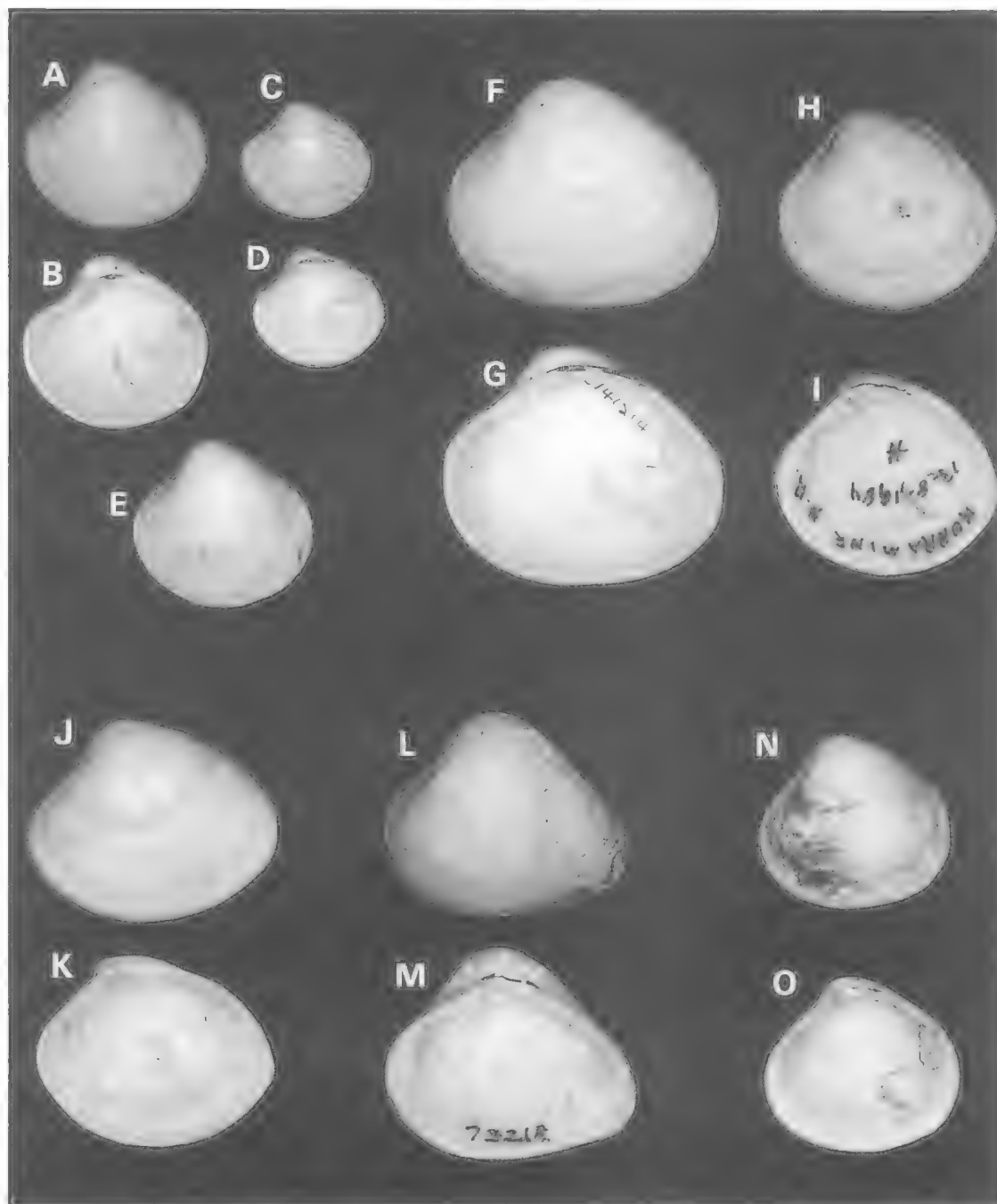


FIG. 7. A-E, *P. (Pitarina) lineolatus* (Sowerby). A, B, KL, Torres Strait, 24mm. A, external lv; B, internal rv. C, D, KL, Palm Is, NEQ, juvenile, 17mm. C, external lv; D, internal rv. E, KL, Torres Strait, external lv, 24mm. F, G, *P. (P.) bullatus* (Sowerby), AMSC141214, Broome, northern WA, 36.2mm. F, external lv; G, internal rv. H, I, *P. (P.) sulfureum* Pilsbry, KL, Kurrimine Beach, NEQ, 28.9mm. H, external lv; I, internal rv. J, K, *P. (P.) coxeni* (Smith), KL, Shelburne Bay, NEQ, 13.5mm. J, external lv; K, internal rv. L, M, *P. (P.) inconstans* (Hedley), AMSC073218, Madang, PNG, 22.1mm. L, external lv; M, internal rv. N, O, *P. (P.) regularis* (Smith), AMSC306561, Magnetic Is, NEQ, 15.5mm. N, external lv; O, internal rv.

**MATERIAL EXAMINED.** HOLOTYPE: 1pv, AMSC113277, off Karumba, SE Gulf of Carpentaria, northern Qld, 17°30'S, 140°00'-141°00'E, 1963-4. Length of shell 46.8mm, height 36.4mm, width of conjoined valves 26.8mm. PARATYPE: 2rv, 1lv, AMSC308642, Gulf of Carpentaria, northern Qld, 1980; 1rv, AMSC74865, Gulf of Papua, PNG, Feb 1969; 1pv, AMSC14952, Karumba, northern Qld, 17°29'S, 140°50'E, beach, Jun 1903; 2pv, AMSC107015, AMSC107028, off Albert River, Gulf of Carpentaria, northern Qld, 17°24'S, 139°47'E, Dec 1963; 1pv, AMSC107296, W of Topsy Creek, E Gulf of Carpentaria, northern Qld, 15°28'S, 141°28.7'E, Dec 1876; 1pv, AMSC115732, 7km from Norman River mouth, Karumba, northern Qld, 17°29'S, 140°50'E, washed from river bank; AMSC117072, off Karumba, SE Gulf of Carpentaria, northern Qld, 17°30'S, 140°00'-141°00'E.

**HABITAT AND DISTRIBUTION.** Buried in sandy mud near mouths of rivers; ranging from northern Queensland to Papua New Guinea.

**REMARKS.** *Pitar (Pitarina) thornleyae* sp. nov. is most similar to *P. (P.) trevori* Healy & Lamprell, 1990, *P. (P.) pellucidus* (Lamarck, 1818) and *P. (P.) subpellucidus* (Sowerby, 1851) in being elongate-ovate and moderately inflated but is readily separated by its larger size, much stronger concentric ridges, longer posterodorsal margin, triangular shaped pallial sinus (wide and short in *P. (P.) pellucidus* and *P. (P.) subpellucidus*, short and ascending in *P. (P.) trevori*). There are no other known Australian *Pitar* species which have the strong concentric ridges of *P. (P.) thornleyae*.

***Pitar (Pitarina) lineolatus* (Sowerby, 1854)**  
(Fig. 7A-E; 10C)

*Cytherea lineolatus* Sowerby, 1854: pl. 168, figs 214-5; *Pitar (Pitarina) lineolatus* Habe, 1977: 257; Lamprell & Whitehead 1992: pl. 67, sp. 524.

**DIAGNOSIS.** Shell length to 24mm, ovate. Sculpture of fine concentric striae. Colour cream, usually with zigzag markings on the escutcheon, lunule, and sometimes faintly on the rest of the shell.

**MATERIAL EXAMINED.** 1pv, KL, Torres Strait, northern Qld, dredged to 15m; 2pv, KL, Palm I, NEQ, dredged in Curacoa Channel to 15m; 1lv, KL, Little Trunk Reef, NEQ, dredged to 10m, Dec 1995.

**HABITAT AND DISTRIBUTION.** Dredged in sand to 16m; ranging from Japan, to northern Queensland and the Torres Strait, Australia.

**REMARKS.** *Pitar (Pitarina) lineolatus* (Sowerby, 1854) is similar to *P. (P.) limatula* (Sowerby, 1853) but readily separated by the cream-white colour and tan zigzag pattern on the lunule and dorsal margin (yellow coloured with black staining on lunule and escutcheon on *P. (H.) limatula*).

***Pitar (Pitarina) bullatus* (Sowerby, 1851)**  
(Fig. 7E,G; 10D)

*Cytherea bullata* Sowerby, 1851: p.640, sp.96, pl. 136, fig. 192; Lamprell & Whitehead 1992: pl. 67, sp. 531.

**DIAGNOSIS.** Shell length to 36.2mm, solid, broadly subtrigonal, inflated, with large inflated umbones. Sculpture of fine concentric striae and growth lines. Colour chalky white externally; interior white.

**MATERIAL EXAMINED.** 17pv, KL, Turkey Beach, central Qld, on sand/mud flats low tide; 1pv, KL, Dingo Beach, central Qld, sand flats low tide; 1pv, KL, Gladstone, southern Qld, on sand flats, Jan 1976; 1pv, KL, Dampier, northern WA, 1987; 1pv, AMSC141214, Broome, northern WA, 17°58'S, 122°14'E; 4pv, AMSC051544, AMSC093530, Roebuck Bay, Broome, northern WA, 18°00'S, 122°15'E; 1pv, KL, Black Ledge, Broome, northern WA, on mud/sand flats, 1994; 4pv, KL, Broome, northern WA, on sand/mud flats.

**HABITAT AND DISTRIBUTION.** Buried in shallow littoral sand/mud flats; ranging in Australia from Queensland, Northern Territory to northern Western Australia.

**REMARKS.** *Pitar (Pitarina) bullatus* (Sowerby, 1851) can be readily separated from other Australian *Pitar* species by its solid, chalky, elongate-ovate shell and straight ventral margin.

***Pitar (Pitarina) sulfureum* Pilsbry, 1904**  
(Fig. 7H,I; 10E)

*Pitar (Pitarina) sulfureum* Pilsbry, 1904: 553, pl. 39; Lamprell & Whitehead 1992: pl. 68, sp. 532.

**DIAGNOSIS.** Shell to length 30mm, light, inflated; almost chalky; escutcheon ill-defined but protrusive. Sculpture smooth, indistinct, fine striae. Colour yellow-cream; umbones yellow, sometimes tinged pink; interior cream-white, light-yellow centrally.

**MATERIAL EXAMINED.** 2lv, AMSC306570, SW of Losuia, Kiriwinna I, Trobriand Group, PNG, 8°33'S, 151°04'E, on sand flats, Jun 1970; 2pv, AMSC306552, SE of Exmouth Homestead, Exmouth Gulf, northern

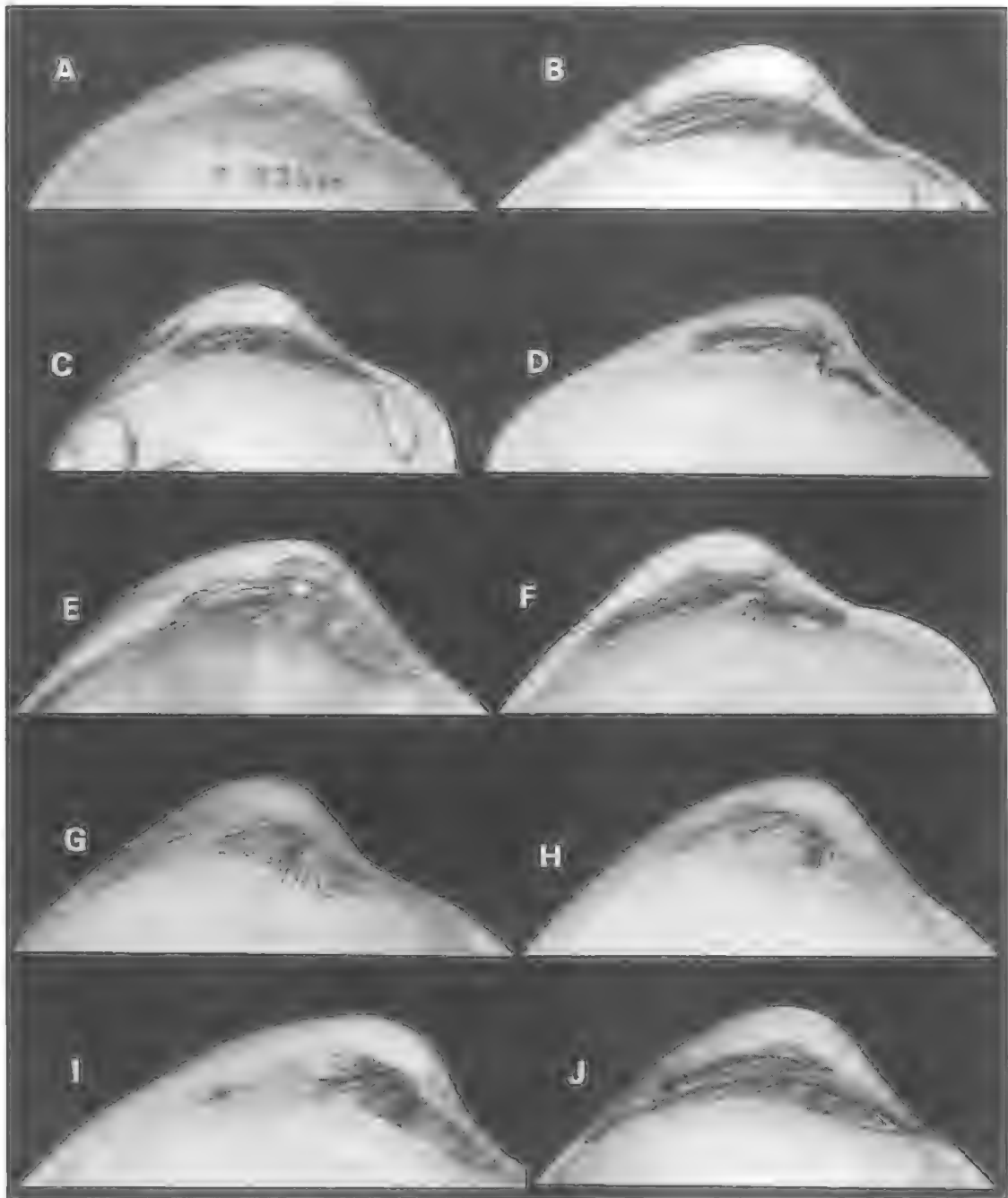


FIG. 8. Comparative hinge plate and teeth of rv. A, *P. (Hyphantosoma) intricata* (Dautzenberg), AMSC123340, 52.5mm; B, *P. (H.) spoori* Lamprell & Whitehead, holotype, AMSC133572, Bank Reef NEQ, 31mm; C, *P. (H.) limatula* (Sowerby), KL, Dingo Beach, central Qld, 24.2mm; D, *P. (H.) caperi* sp. nov., holotype, AMSC202973, Upolu Cay, NEQ, 22.8mm; E, *P. (P.) citrina* (Lamarck), KL, Shark Bay, northern WA, 45.4mm; F, *P. (H.) nancyae* Lamprell & Whitehead, off Caloundra, Qld, 28.6mm; G, *P. (P.) osmunda* (Iredale) AMSC303944, Sydney Harbour, 36.5mm; H, *P. (P.) curnowae* sp. nov., holotype, AMSC202974, Madang, PNG, 42.6mm; I, *P. (P.) prora* (Conrad) KL, North West Is, Qld, 63mm; J, *P. (P.) marrowae* Healy & Lamprell, QMMO32900, Dingo Beach, central Qld, 38.1mm.

WA, 22°24'S, 114°08'E, on muddy sand flats; 2pv, KL, Kurrimine Beach, NEQ, low tide on sand.

**HABITAT AND DISTRIBUTION.** Buried in loose shallow muddy sand flats; ranging from Japan to Papua New Guinea and Queensland.

**REMARKS.** *Pitar (Pitarina) sulfureum* Pilsbry, 1904 is recognised by its rough surface and dense, fine concentric striae and chalky yellow-cream appearance. In these respects it is most similar to *P. (P.) bullatus* (Sowerby, 1851) but differs by having a convex ventral margin (almost straight in *P. (P.) bullatus*). *P. (P.) bullatus* also has a rough surface and dense, fine concentric striae and chalky white appearance. However *P. (P.) sulfureum* differs from *P. (P.) bullatus* by having a convex ventral margin (almost straight in *P. (P.) bullatus*). *P. (P.) sulfureum* appears to be a rare species in Australia with few specimens either in the Museum or private collections.

***Pitar (Pitarina) coxeni* (Smith, 1885)  
(Fig. 7I,K; 10F)**

*Cytherea (Caryatis) coxeni* Smith, 1885: 139, pl. 1, figs 7-7e; *Pitar (Pitarina) coxeni* Lamprell & Whitehead, 1992: pl. 68, sp. 530.

**DIAGNOSIS.** Shell length to 13mm, thin, ovate, moderately obese. Sculpture of fine, close, distinct concentric striae, often polished. Colour white, internally and externally; obscure brown or red lines and dots or pale growth lines sometimes occur.

**MATERIAL EXAMINED.** 1pv, KL, Whitsunday Passage, central Qld, trawled to 10m; 2pv, KL, Shelburne Bay, NEQ, 12°39.4'S, 141°09'E, 41m, Jan 1993.

**HABITAT AND DISTRIBUTION.** Dredged in sand to 25m; ranging from central Queensland to the Northern Territory and Papua New Guinea.

**REMARKS.** *Pitar (Pitarina) coxeni* (Smith, 1885) is very fragile and rare even in Museum collections. *P. (P.) coxeni* is most similar to *P. (P.) sophiae* (Angas, 1877) in size, shape and fragility, but differs in having a more attenuate posterior margin and angulate pallial sinus (posterior margin widely convex and pallial sinus widely rounded in *P. (P.) sophiae*).

***Pitar (Pitarina) inconstans* (Hedley, 1923)  
(Fig. 7L,M; 10H)**

*Pitar (Pitarina) inconstans* Hedley, 1923: 304; Lamprell & Whitehead, 1992: pl. 68, sp. 529.

**DIAGNOSIS.** Shell length to 20mm, inflated, subtriangular, posteriorly attenuate. Sculpture fine, almost polished, concentric growth lines. Colour white, sometimes with grey growth bands; interior white.

**MATERIAL EXAMINED.** 1pv, AMSC073218, Madang, PNG, 5°02.5'S, 145°7'E; 3pv, KL, Buffalo Creek, Darwin, NT, 1984; many, KL, Nanum Beach, Weipa, NEQ, Jul 1992, N. Trevor; 3pv, KL, Numbulwar, Gulf of Carpentaria, NT, 1984.

**HABITAT AND DISTRIBUTION.** In shallow littoral sand; ranging in Australia from north Queensland and the Northern Territory to Papua New Guinea and Malaysia.

**REMARKS.** *Pitar (Pitarina) inconstans* (Hedley, 1923) is quite variable in shape and remarkably similar to the mactrid *Notospisula trigonella* (Lamarck, 1819) which is equally variable in shape but is readily separated from that species by the hinge teeth.

***Pitar (Pitarina) regularis* (Smith, 1885)  
(Fig. 7N,O; 10G)**

*Cytherea (Caryatis) regularis* Smith, 1885: 140, pl. 1, figs 8-8b; *Pitar (Pitarina) regularis* Lamprell & Whitehead, 1992: pl. 68, sp. 528.

**DIAGNOSIS.** Shell length to 19mm, compressed. Sculpture of close-set concentric ridges, slightly lamellate posteriorly. Colour off-white with rust-brown concentric bands.

**MATERIAL EXAMINED.** 1pv, AMSC306561, Horseshoe Bay, Townsville, NEQ, 19°06.8'S, 146°51.8'E, Sep 1980; 2pv, 2lv, AMSC306535, off Broad Sound, central Qld, 22°06'S, 150°49'E, 53m, among coarse shell, Dec 1977; 1v, AMSC306531, off Cairns, NEQ, 16°55'S, 146°07'E, 37-40m, sandy shell and mud; 2pv (juvenile), AMSC306530, Arafura Sea, NE of Croker I., NT, 10°36'S, 132°56.5'E, 62m; 1pv, KL, Boyne I., Qld, beach; 1pv, KL, Gulf of Carpentaria, NT, Bureau of Rural Resources, 1990.

**HABITAT AND DISTRIBUTION.** In littoral sand and dredged in sandy mud and coarse shell to 62m; ranging from Hong Kong, West Malaysia to Australia, north Queensland, Torres Strait, Northern Territory and north Western Australia.

**REMARKS.** *Pitar (Pitarina) regularis* (Smith, 1885) is most similar to *P. (P.) bullatus* (Sowerby, 1851) in being solid, having a rough, chalky surface, fine concentric growth lines and white colour. *P. (P.) regularis* differs in the ventral margin being convex (straight in *P. (P.) bullatus*).

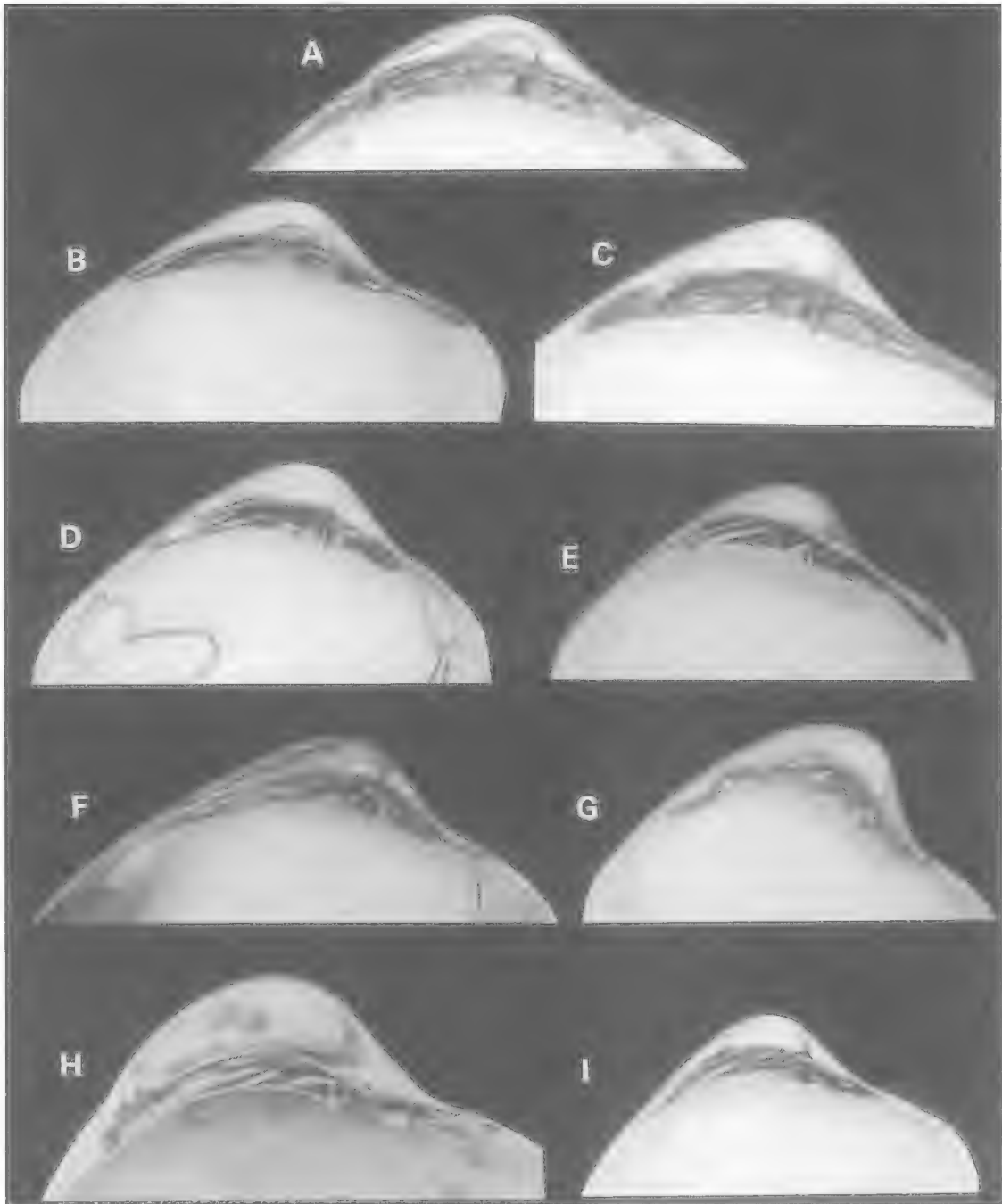


FIG. 9. Comparative hinge plate and teeth of rv. A, *P. (Pitarina) affinis* (Gmelin) KL, Shark Bay, northern WA, 55.8mm; B, *P. (P.) pellucidus* (Lamarck) KL, Dingo Beach, central Qld, 34.4mm; C, *P. (P.) potteri* Healy & Lamprell, holotype, QMMO32902, Shelly Beach, NEQ, 38mm; D, *P. (P.) trevori* Lamprell & Whitehead, holotype, QMMO22850, Dingo Beach, central Qld, 30mm; E, *P. (P.) queenslandica* sp. nov., holotype, AMSC306560, Black Is, NEQ, 21mm; F, *P. (P.) subpellucidus* (Sowerby) KL, St Crispins Reef, NEQ, 33mm; G, *P. (P.) japonicus* Kuroda & Kawamoto, AMSC095267, south of Yeppoon, Qld, 37.6mm; H, *P. (P.) noguchii* Habe, AMSC121360, Roebuck Bay, Broome, WA; I, *P. (P.) nipponica* Kuroda & Habe, AMSC306563, Shelley Beach, Townsville, NEQ, 27.3mm.

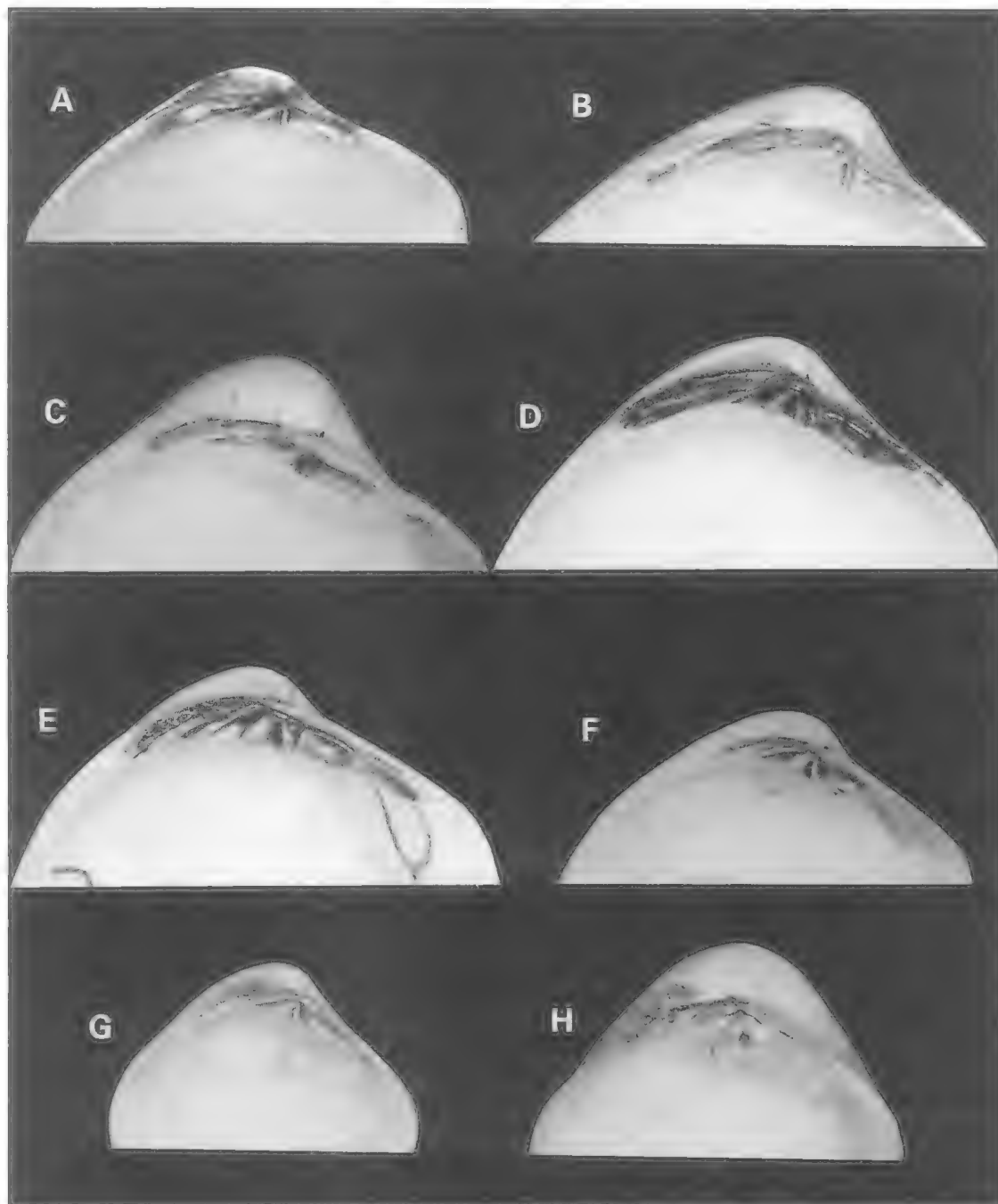


FIG. 10. Comparative hinge plate and teeth of rv. A, *P. (Pitarina) sophiae* (Angas), AMSC007545, Port Jackson, NSW, 23.2mm; B, *P. (P.) thornleyae* sp. nov., holotype, AMSC113277, Karumba, Gulf of Carpentaria, NEQ, 46.8mm; C, *P. (P.) lineolatus* (Sowerby), KL, Torres Strait, 24mm; D, *P. (P.) bullatus* (Sowerby), AMSC141214, Broome, northern WA, 36.2mm; E, *P. (P.) sulfureum* Pilsbry, KL, Kurrimine Beach, NEQ, length 28.9mm; F, *P. (P.) coxeni* (Smith), KL, Shelburne Bay, NEQ, 13.5mm; G, *P. (P.) regularis* (Smith), AMSC306561, Magnetic Is, NEQ, 15.5mm. H, *P. (P.) inconstans* (Hedley), AMSC073218, Madang, PNG, 22.1mm.



having coarser concentric lines and is less inflated than that species.

### ACKNOWLEDGEMENTS

The authors extend their thanks to Mr I. Loch (Australian Museum) for allowing us to examine and borrow material for this project and to Dr H. Saito (National Science Museum, Tokyo) for organising loan of the holotype of the holotype of *P. (P.) nipponica* from the Imperial Collection. Mrs G. Curnow (South Australia) and Mr P. Spoor (Townsville) are thanked for donating or lending specimens for study. Special thanks to Dr John Stanisic for reading the manuscript and valuable advice. This work was supported by a Keith Sutherland Award to KL. An Australian Research Fellowship and a Senior Research Fellowship from the Australian Research Council made possible the participation of JH.

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A NEW STREAM-DWELLING *LITORIA* FROM THE MELVILLE RANGE,  
QUEENSLAND, AUSTRALIA

KEITH R. McDONALD

McDonald, K.R. 1997 06 30: A new stream-dwelling *Litoria* from the Melville Range, Queensland, Australia. *Memoirs of the Queensland Museum* 42(1): 307-309. Brisbane. ISSN 0079-8835.

*Litoria andiürrmalin* sp. nov. (Anura: Hylidae) is described from streams amongst boulders in Cape Melville National Park, Queensland. It is a large, mottled brown species with unwebbed fingers, extensively webbed toes and distinct supratympanic fold: females have pigmented eggs. The species is found in boulder areas around riffles in streams. Morphologically it cannot be referred to any recognised Australian hylid species group. □ *Frog, Hylidae, Litoria, Queensland, Litoria andiürrmalin.*

Conservation Strategy Branch, Department of Environment, PO Box 834, Atherton, Queensland 4883, Australia; 6 March 1997.

During botanical surveys in Cape Melville National Park on Cape York Peninsula, Queensland in 1993, a specimen of unidentified hylid frog was caught along a rocky, rainforest stream by J.P. Stanton. Examination of the juvenile specimen indicated it was possibly an undescribed species. In May 1994 the opportunity to re-visit the collection site was made possible during a botanical survey led by D.G. Fell. Adult specimens were collected and the species was confirmed as undescribed. The species is described in this paper. It is a hylid frog of the genus *Litoria* having expanded finger and toe discs with a distinct notch, horizontal pupil and no palpebral venation on the lower eyelids.

Methods of measurement follow Tyler (1968). Measurements were made using dial calipers reading to an accuracy of 0.1 mm. Measurements were: S-V, body length from snout to vent; TL, tibia length; HL, head length; HW, head width; E-N, eye to naris length; IN, internarial span; E, eye diameter; T, tympanum diameter. Specimens are lodged in the Queensland Museum, Brisbane (QMJ), Australian Museum, Sydney (AMR) and the South Australian Museum, Adelaide (SAMR).

***Litoria andiürrmalin* sp. nov.**

*Litoria* species, Frith and Frith, 1995: 233.

**MATERIAL EXAMINED.** HOLOTYPE: QMJ59000 adult ♀, collected by K.R. McDonald, J.A. Ledger and D.G. Fell at 280m, 2 May 1994 at Temple Ck on the eastern slopes of the Melville Range, Cape Melville National Park (144°31'E, 14°16'S). PARATYPES: QMJ59001-008, AMR144391, SAMR44463 same data as holotype, QMJ59009 collected by J.P. Stanton and D.G. Fell, 21 July 1993 at type locality.

**DIAGNOSIS.** A large species (preserved specimens 93-102mm N=5; field measurements of live animals; ♀♀ 92.3-109.7mm, N= 6; ♂♂ 66.1-75.6mm, N=9, S-V) characterised by widely expanded finger and toe discs; moderately long hindlimbs; unwebbed fingers; extensively webbed toes; absence of dermal glands; strong supratympanic fold; in life mottled brown with irregular cream markings and pale dorsolateral stripe from eye bulge to groin.

**DESCRIPTION OF HOLOTYPE.** Head flattened, slightly broader than long (HL/HW 0.90); head length about 1/3 snout to vent length (HL/S-V 0.35).

Snout not prominent, slightly rounded in profile, canthus rostralis distinct, slightly curved. Nostrils lateral, their distance to snout slightly less than distance between eye and naris (E-N/IN 1.46).

Eye prominent, slightly larger than eye to naris distance. Tympanum large with narrow annulus, diameter 0.6 width of eye. Vomerine teeth on two large elevations between posterior margin of choanae. Tongue broadly oval.

Fingers moderately long, slender and unwebbed; finger lengths 3>4>2>1; terminal discs large.

Hindlimbs moderately long (TL/S-V 0.57); toe lengths 4>3>5>2>1. Web reaches base of terminal disc on all toes except 4th; reaches top of subarticular tubercle at base of penultimate phalanx on 4th toe; prominent inner metatarsal tubercle; no outer metatarsal tubercle.

Skin of dorsum smooth. Strong supratympanic fold extends beyond superior margin of tympanum. Ventral surface coarsely granular. In life dorsum mottled brown with irregular cream

markings and an indistinct pale dorsolateral stripe from eye bulge to groin; posterior ventral surface cream, throat faintly greyish to junction of arms.

Dimensions of the holotype in mm: S-V 99.44; HL 35.14; HW 39.14; TL 56.38; E-N 10.46; IN 7.2; E 10.48; T 6.24.

**VARIATION.** The overall proportions of the 11 paratypes are similar (HL/HW 0.90-1.11; HL/S-V 0.34-0.40; E-N/IN 1.19-1.79). Hand and toe webbing has no detectable variation. In life low tubercles on the back, eye bulge and around the nostrils are evident in some animals.

The juvenile frog (QMJ59009) has a distinctly dark throat with a pale line on the mid-throat. The dark throat pales to a light grey in adults. In life a dorsolateral stripe extends from the eye bulge to groin, becoming less distinct in larger frogs. Juveniles are light cream with dark markings laterally. These fade with increasing size.

Males possess dark brown, glandular nuptial pads and lack a vocal sac.

**ETYMOLOGY.** The specific name, *andirrmalin*, is from the Barrow Point Aboriginal language, Gambilmugu, for the frog (Roger Hart pers. comm., Aboriginal elder and cultural informant). Mr Hart explains that in local tradition the frogs are people who have been transformed as punishment for breaching certain rules. The species and habitat are believed to be culturally sensitive by Aboriginal people of the area.

**COMPARISON WITH OTHER SPECIES.** The combination of large size, no webbing on the slender fingers, full webbing on the toes, strong supratympanic fold and colouration is not shared by any species groups defined by Tyler & Davies (1978). The general appearance of body shape when first observed is similar to *Litoria caerulea*. However *L. andirrmalin* lacks the large parotoid glands and finger webbing of *L. caerulea*. Members of the *Litoria citropa* species group have moderately long, slender unwebbed fingers like *L. andirrmalin* but do not possess full toe webbing or a well-defined supratympanic fold and are much smaller.

#### NATURAL HISTORY

*Litoria andirrmalin* was observed near cascades and riffles but not pools, in perennial streams above 60m in the Melville Range. The streamside vegetation is mesophyll vine forest with *Melaleuca* emergents occurring as gallery forest. Large granite boulders and bedrock of the Permian Altonmoui Granites are a feature of the stream habitat.

The frog was observed on rocks, vines and twigs adjacent to broken water. It did not jump into the stream to escape when disturbed but preferred to climb under boulders or into vegetation. When placed in running water or pools the frog immediately swam to the bank, and jumped into the adjacent habitat. It did not attempt to escape into the stream like stream frogs of the Wet Tropics Biogeographic Region (e.g., *Litoria nanotus*, *Taudactylus acutirostris*, unpubl. obs.)

A ♀ (QMJ59002) had small (1mm) pigmented eggs in May 1994. Other ♀♀ observed in the field in October, 1994 and November, 1995 also had eggs. ♀♀ examined in mid to late February 1995 had no eggs suggesting breeding takes place between early December to mid February coinciding with the onset of the monsoonal wet season. ♀♀ carry eggs at least from May to at least the onset of the monsoon season. Similar carrying of eggs outside the breeding season has been documented (McDonald & Davies 1990).

Males were calling in late November, 1995. The call sounds like tapping with a stick on a piece of bamboo, a rapid, gentle 'toc toc toc toc'. No calling was heard in other months.

No tadpoles of any species were observed in the stream or pools in May, October, November or February. An undescribed species of *Cophixalus* was located in the boulders adjacent to the stream habitat of *L. andirrmalin* and adult *Rana daemeli* and *Litoria infrafrenata* were observed in the same stream habitat. In February 1995 *L. infrafrenata*, *L. caerulea* and *R. daemeli* were calling near and adjacent to the stream whilst juveniles of *L. andirrmalin* and *R. daemeli* were present in May and October also indicating possible monsoonal-season breeding.

Examination of contents of two faecal pellets deposited overnight disclosed a leaf, an unidentified small frog, freshwater prawn legs (*Macrobrachium* sp.) and beetle remains. Flushed stomach contents from five frogs revealed a litter skink *Lygisaurus* sp., coleopteran larva, beetle and cockroach remains.

#### DISTRIBUTION AND CONSERVATION STATUS

The species is restricted to streams in the Melville Range which is part of the greater Laura Basin, and an area of higher rainfall than the adjacent areas of Cape York. This is especially so on the coast which is influenced by the orientation of the coastal ranges and prevailing south east winds. The Melville Range in Cape Melville Na-

tional Park is a distinct geological feature of Altonmoui granites supporting a unique combination of rainforest and sclerophyll forest communities with affinities closer to the McIlwraith Range than to the Wet Tropics biogeographic region (J.P. Stanton, pers. comm.). The greater Laura Basin, including the eastern escarpments and isolated ranges largely in Starke Pastoral Holding and the dune system of Cape Flattery, includes endemic species of skinks found on sandstone, granite or silica sands — *Lerista ingrami*, *Ctenotus quinkan*, *Ctenotus rawlinsoni*, *Ctenotus nullum*, *Carlia dogare* and *Cryptoblepharus fuhni* and a boulder-inhabiting frog, *Cophixalus* sp. nov.

The geological formations, vegetation types and climatic conditions are atypical for Cape York and Wet Tropics biogeographic regions (Stanton & Morgan 1977) indicating that the area should be recognised as a distinct biogeographic region, as reflected in the unique assemblages and endemic species of fauna and flora.

The habitat of *Litoria andiirrmalin* is restricted within a conservation land tenure which is not threatened at this stage. The conservation status would be 2R (rare and restricted to less than 100km) using the criteria of McDonald et. al. (1991). Other species endemic to the Melville Range are the skink *Cryptoblepharus fuhni* (Roberts 1994), an undescribed frog *Cophixalus* sp., the Foxtail Palm (*Wodyetia bifurcata*) and the tree *Acmenosperma pringlei*.

#### ACKNOWLEDGEMENTS

I am indebted to Peter Stanton who drew my attention to frogs in the Cape Melville area and made it possible to re-visit the site of his original collection. Dave Fell, Juliana Ledger, Clifford Frith, Rob Worrall and Les Jackson assisted in the field and in various ways. Priscilla Gibson, Peter Sutton and Roger Hart gave helpful guidance

with names used by the aboriginal people in the Cape Melville area for frogs. Roger Hart also gave permission for the the name and the aboriginal story to be told. Jeanette Covacevich, Dr Marg Davies, Suzan Horder, and Steve Richards provided helpful advice. Professor Barrie Jamieson and Associate Professor Craig Moritz, Centre for Conservation Biology, University of Queensland provided facilities to complete this work while I was on the Queensland Government Interchange Programme. This assistance is most gratefully appreciated.

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**A RANGE EXTENSION FOR *LITORIA BREVIPALMATA* (ANURA: HYLIDAE).** *Memoirs of the Queensland Museum* 42(1): 310. 1997:- Until 1995 the distribution of *Litoria brevipalmata* was believed to have extended from the SEQ Border Ranges and Darling Downs (McDonald, 1974 collected specimens from Crows Nest and Ravensbourne National Parks) to Brisbane's metropolitan area (Natrass and Ingram, 1993, recorded species at Woogaroo Ck near Wacol, Brisbane), through the extreme coastal lowlands, Glass House Mountains (Hannah & Smith, 1995; Gynther pers. comm.) and Conondale Ranges/Jimna area, Kilcoy Shire (McEvoy et al 1979 and Czechura 1978). In 1996 a new locality for *L. brevipalmata* was recorded in the Brooweena area (near Maryborough, SEQ) constituting a northerly range extension (Natrass pers. comm.). This paper documents a new locality at Yarraman State Forest for *L. brevipalmata*, the most western known locality for this species (approximately 40 km west of Brooweena). Two adults and one juvenile were recorded at Yarraman State Forest 289 (Qld Forestry Map number 9244-2), southeast Queensland. The juvenile was positively identified by G. Ingram (Qld Museum, pers. comm.).

Two adults were observed during a survey conducted on 18 November, 1995, along Rocky Creek (SF 289), after 51.8mm of rain had fallen two days previously. Rocky creek is buffered from surrounding *Araucaria cunninghamii* plantations by dry sclerophyll forest dominated by *Eucalyptus* and *Angophora* spp. with a ground cover predominantly of exotic herbs, grasses and *Lantana camara*. The first adult was observed at a dam (grid reference Forestry 9244-2; 936 314), approximately 200m from Rocky Creek, located about 2 m from the water's edge. The second was observed on an exposed branch of a fallen *Casuarina* overhanging the water upstream of Rock Creek, beside another dam (grid reference Forestry 9244-2; 941 317). Numerous trees, mainly *Casuarina* and *Eucalyptus* spp., were found on the dam wall with a ground cover similar to that at the first dam.

Other species of frogs sighted or heard vocalising here included: *Crinia signifera*, *Limnodynastes terraereginae*,

*Litoria caerulea*, *L. chloris*, *L. dentata*, *L. fallax*, *L. nasuta*, *L. latopalmata*, *L. lesueuri*, *Mixophyes fasciolatus* and *Bufo marinus*. At no time was *L. brevipalmata* heard.

A subsequent survey was conducted on 28 November, 1995, after 59.8mm of rain had fallen between 20 and 23 November. A juvenile was collected 30 cm from the water's edge at the first dam (grid reference Forestry 9244-2; 936 314). It is interesting that no frogs were observed during surveys on 1 October, 1995, or 9 November, 1995, at the dams along Rocky Creek when no rain had fallen previously. It appears that *L. brevipalmata* only becomes active after sufficient rainfall, concurring with observations made R. Natrass (pers. comm.). A final survey conducted on the night of 29 November failed to locate *L. brevipalmata*, although all other frog species present during the previous fortnight's surveys were still found, in low abundance.

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A NEW SEMI-TERRESTRIAL ACOTYLEAN FLATWORM, *MYORAMYXA PARDALOTA*  
GEN. ET SP. NOV. (PLEHNIIDAE POLYCLADIDA) FROM SOUTHEAST  
QUEENSLAND, AUSTRALIA

LESLIE J. NEWMAN AND LESTER R.G. CANNON

Newman, L.J. & Cannon, L.R.G. 1997 06 30. A new semi-terrestrial acotylean flatworm, *Myoramyxa pardalota* gen. et sp. nov. (Plehniiidae, Polycladida) from southeast Queensland, Australia. *Memoirs of the Queensland Museum* 42(1): 311-314. Brisbane. ISSN 0079-8835.

A new acotylean flatworm, *Myoramyxa pardalota* gen. et sp. nov., is described from the high intertidal zone, southeast Queensland, Australia. The family Plehniiidae Bock, 1913 is emended to contain this new monotypic genus which is characterised by possessing eyes around the anterior margin and retractile nuchal tentacles with eyes, but no frontal eyes, no seminal vesicle, and ejaculatory ducts that enter at the side of the large prostate; Lang's vesicle is lacking. The False Water-rat, *Xeromys myoides*, was observed to prey on these worms: this is the first record of a mammal feeding on a polyclad flatworm. □ *Polycladida*, *Acotylea*, *Plehniiidae*, *flatworm*, *taxonomy*.

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Polyclad flatworms are, with one freshwater exception (*Limnostylochus* from Borneo), marine animals (Prudhoe, 1985) where they are well known as predators of invertebrates such as small crustaceans, molluscs and ascidians (Prudhoe, 1985; Cannon, 1986; Newman & Cannon, 1994). Some are even well-known pests of commercial bivalves including rock oysters (Steade, 1907; Jennings & Newman, 1996), pearl oysters and giant clams (Newman et al., 1993) and may pose a threat to these industries. None are known to invade terrestrial habitats.

Though active predators themselves, only three studies report predators of polyclads; these include a polychaete (Riser, 1974), and pufferfish (Poulter, 1975; Jennings & Newman, 1996). That polyclads are unlikely to be attacked or eaten is attributed to their being distasteful according to Prudhoe (1985), presumably because of their toxicity. Studies have shown that some acotylean species contain highly toxic substances such as tetrodotoxin (Jeon et al., 1986; Miyazawa et al., 1987). This may also explain why pufferfish can consume these worms (Flowers, pers. comm.).

This account is of a new monotypic genus of polyclads found in the semi-terrestrial supralittoral zone of Moreton Bay where it is exposed to predation by a mammal, the False Water-rat, *Xeromys myoides*.

#### METHODS

Worms were hand collected from under fallen logs, driftwood and large rocks from the high

intertidal zone from: Myora, North Stradbroke Island (27°27'40"S; 153°25'40"E); Caloundra (26°48'S; 153°08'E) and Pebble Beach, near Bribie Island (27°05'S; 153°08'E), southeast Queensland. Animals were photographed in the laboratory, fixed on frozen polyclad fixative and preserved in 70% ethanol for histological preparations (Newman & Cannon, 1995). Whole mounts were stained with Mayer's Haemalum, dehydrated in graded alcohols and then mounted in Canada balsam. Longitudinal serial sections of the reproductive region were obtained from specimens embedded in Paraplast (56°C), sectioned at 5-7 µm, and then stained with haematoxylin and eosin.

Measurements of the body were taken from live animals in a relaxed state and are given as length mm x width mm. Measurements of the reproductive organs are taken from the paratypes. Reconstruction of the reproductive system is diagrammatic and derived from the sections with minimal interpretation. Drawings were made with the aid of a camera lucida by L.J.N. Specimens were collected and photographed by Bruce Cowell. This material is lodged at the Queensland Museum (QM) as whole mounts (WM), serial sections (LS) and wet specimens (S).

#### PLEHNIIDAE Bock, 1913

##### *Myoramyxa* gen. nov.

**DIAGNOSIS.** Plehniiidae with marginal eyes in 3 to 4 rows anteriorly, becoming less numerous

about 1/3 of the way posteriorly along the margin. Frontal eyes absent. Possessing nuchal tentacles.

**ETYMOLOGY.** Named *Myora* for its type location and *myxa* = slime (L. fem.) for its ability to produce copious amounts of mucus.

**TAXONOMIC REMARKS.** As presently diagnosed ( $\delta$  reproductive system without prostates, ejaculatory duct enters the side of the prostate, no seminal vesicle;  $\gamma$  system with ductus vaginalis with large ruffled antrum) Plehniidae contains worms lacking nuchal tentacles (Prudhoe, 1985; Cannon, 1986). The rather unusual and distinctive insertion of the ejaculatory duct into the side of the prostate distinguishes the Plehniidae from all other polyclads. *Myoramyxa* clearly has this character. We believe it is appropriate to emend the family diagnosis to include worms with or without nuchal tentacles. It should be noted that nuchal tentacles may not always be seen in poorly fixed material and may have been overlooked previously.

Within the Plehniidae this genus is similar to *Discocelides* Bergendal, 1893, however, *Myoramyxa* lacks a Lang's vesicle.

***Myoramyxa pardalota* sp. nov.**  
(Figs 1, 2A-C)

**MATERIAL EXAMINED.** HOLOTYPE. *Myora*. Stradbroke Is., southeast Qld, under logs and rocks, high intertidal, 04.05.92, S. Van Dyke WM, QMG210875. PARATYPES. Same data, S, QMG210878; 12.05.92, LS, QMG210874; 19.07.92, LS, QMG210876; S, QMG210808; WM, QMG210877; Pumistone Passage, Caloundra, SE Qld, under log, high intertidal, 07.10.93, P. Davie, LS, QMG210873; Pebble Beach, Bribie Is., SE Qld, 05.11.92, L. Newman & Z. Khalil, LS, QMG210872.

**DESCRIPTION.** Dorsal surface light brown with dark brown leopard spots (composed of microdots) closely packed in a dense pattern, darker brown medially forming a narrow, longitudinal line (Fig. 1). Ventral surface light orange-brown, darker medially with some dark brown pigment surrounding the mouth and gonopores.

Body round oval, thick and fleshy. Nuchal tentacles short, conical, retractile and relatively small, with about 40-50 eyes inside each tentacle, eyes absent at the base (Fig. 2A,B). Marginal eyes in 3 (or 4) rows anteriorly, becoming less numerous (to 2 rows) about 1/3 of the way along the margin. About 150-200 cerebral eyes between the tentacles, no frontal eyes. Pharynx oval, central, mouth posterior, extending approx. 1/3 the length of the body. Gonopores posterior to the pharynx.  $\delta$  pore



FIG. 1. Live *Myoramyxa pardalota*, gen. et sp. nov., holotype (QMG210875): dorsal (top) and posterior ventral views. (Photo by B. Cowell)

small, anterior and close to the  $\gamma$  pore; ductus vaginalis well separated from gonopores, large ruffled antrum. Size range 30mm x 25mm (mature) to 35mm x 25mm (mature).

Large prostate (1.8 mm), seminal vesical lacking, spermaducal bulbs joining ejaculatory duct which enters laterally into the prostate. Penis papillae wide, without stylet.  $\delta$  antrum narrow and deep.  $\gamma$  antrum deep and ruffled. Vagina leads dorsoanteriorly, then is highly coiled posteriorly until it leads into a voluminous, muscular, swollen ductus vaginalis.

**DIAGNOSIS.** With characters of the genus and a dorsal surface with dark pattern of brown spots like a leopard with a narrow, dark median line.

**ETYMOLOGY.** Named *pardalota* = spotted like a leopard (L. fem.) for its spotted dorsal colour pattern.

**HABITAT & DISTRIBUTION.** Common inside or under hardwood logs, driftwood or rocks in the high intertidal (supralittoral) zone particularly with adjacent mangroves from Moreton Bay, SE Queensland.

**DISCUSSION.** The Plehniidae are somewhat aberrant members of the Stylochoidea (*sensu* Prudhoe, 1985) in that they frequently have few or no eyes anteriorly. The distinctive manner in which the ejaculatory duct joins at the side of the

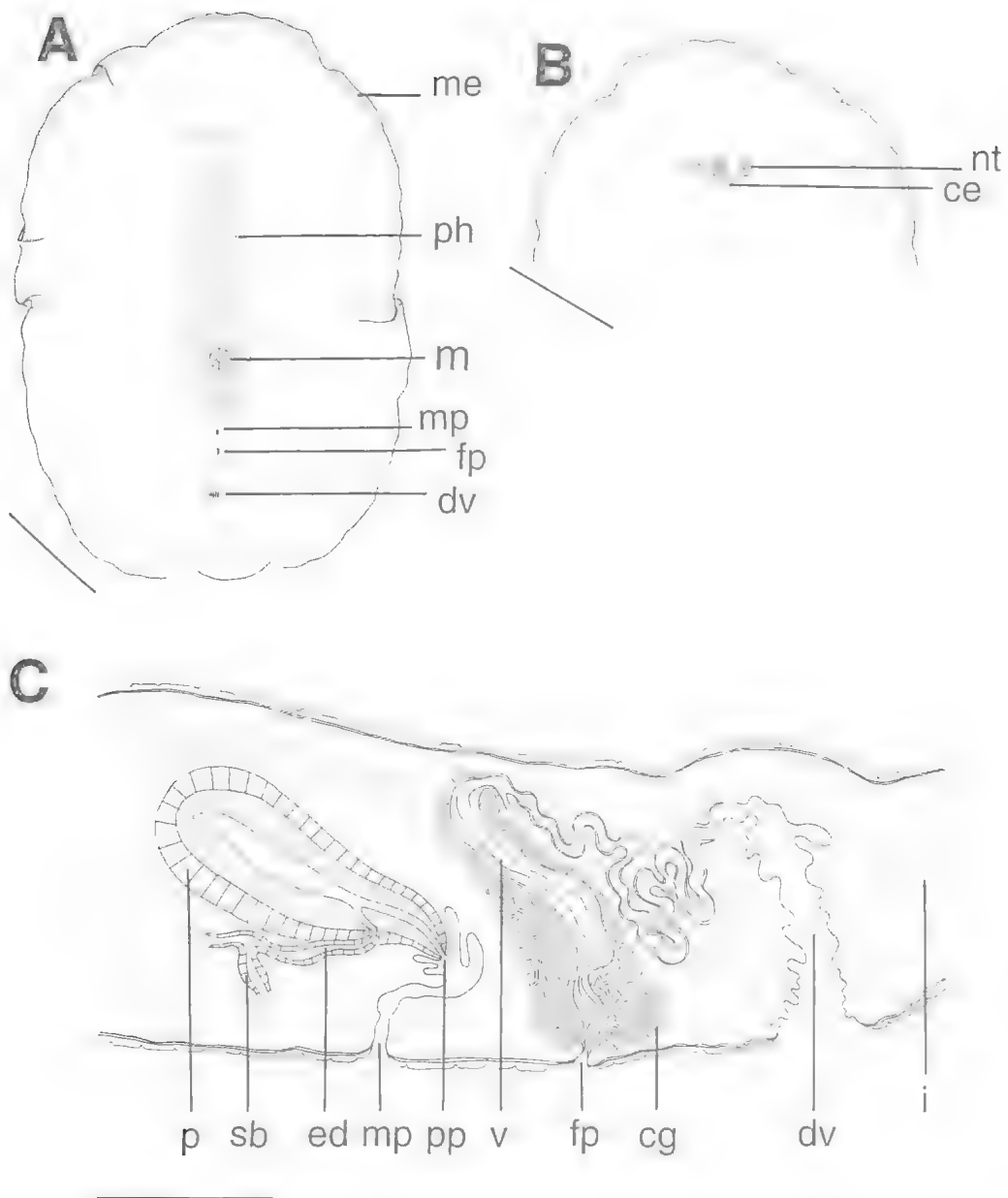


FIG. 2. *Myoramyxa pardalota*, gen. et sp. nov.: A, holotype (QMG210875), wholemount of the ventral side and B, eye arrangement from the dorsal side; C, paratype (QMG210876), diagrammatic representation of the reproductive anatomy. Scales: A,B, 5mm; C, 1mm. (Legend: ce = cerebral eyes, cg = cement glands, dv = ductus vaginalis, ed = ejaculatory duct, fp = ♀ pore, i = intestine, m = mouth, me = marginal eyes, mp = ♂ pore, nt = nuchal tentacles, p = prostate, ph = pharynx, pp = penis papilla, sb = spermaductal bulb, v = vagina).

prostate, however, would seem to be a synapomorphy for the group. Characters such as the presence of nuchal tentacles, which could so easily be overlooked, we believe should not be over-

emphasised. Consequently, we consider the emendation of the family Plehniidae to be justified and a more conservative approach than erection of a new family at this time.



These worms were brought to our attention by Steve Van Dyck who had found them being eaten, with apparent relish, by the False Water-rat, *Xeromys myoides* (see figure p. 36-7) (Van Dyck, 1994). The rat forages at night in the supralittoral and littoral at the upper influence of the tide. During the day worms are found in sheltered locations quite out of water such as the moist inside or underside of hardwood logs thrown up as driftwood in the supralittoral zone; as many as 14 worms have been found clustering together.

In the laboratory worms actively retreat from water, if placed in it and given the opportunity to crawl out. They produce copious amounts of clear mucus which surrounds the resting animal like a jelly coat. In the field their presence is revealed by slime trails similar to those produced by slugs and snails. Presumably these animals emerge at night to forage on small invertebrates. They are clearly semi-terrestrial which has evidently exposed them to predation.

Many polyclads are known to be highly toxic: it remains to be seen if *Myoramyxa* is toxic particularly since the rat evidently finds them delectable.

#### ACKNOWLEDGMENTS

We wish to thank S. Van Dyke for finding this unusual worm and P. Davie and Z. Khalil for collecting additional specimens. Specimens were prepared for histology by Z. Khalil and curated by K. Sewell. B. Cowell kindly photographed live animals. Financial support was generously provided to L.J.N. by the Australian Biological Resource Study, Canberra. We would also like to thank the Queensland Museum and the Zoology Department, University of Queensland.

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# OSTEOLOGY OF IMMATURE DARK SHOULDER MINKE WHALES *BALAENOPTERA ACUTOROSTRATA* FROM SOUTHERN QUEENSLAND

R.A. PATERSON, H.A. JANETZKI AND S.C. WILLIAMS

Paterson, R.A., Janetzki, H.A. & Williams, S.C. 1997 06 30: Osteology of immature dark shoulder minke whales *Balaenoptera acutorostrata* from southern Queensland. *Memoirs of the Queensland Museum* 42(1): 315-325. Brisbane. ISSN 0079-8835.

Osteology of a physically immature 6.02m long dark shoulder minke whale *Balaenoptera acutorostrata* is described as well as its baleen. Comparison is made with the skulls of three other less mature dark shoulder forms in the Queensland Museum collection and problems associated with reliance on osteological features of non-adult specimens are discussed. □  
*Minke whale, Balaenoptera acutorostrata, osteology.*

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On 27 August 1995 a minke whale carcass was found drifting in the Great Sandy Strait near Boonooroo (25°40'S, 152°54'E). It was retrieved the following day and flensed by a Queensland Museum team on 29 August. By then, this 6.02m long whale had decomposed and its skin had extensively sloughed. Identification as a dark shoulder or Antarctic form, described as Type 1 or 2 by Best (1985), was made on baleen appearances and not from external features. The entire skeleton, with the exception of the pelvic bones, was recovered together with the baleen and larynx. The specimen is registered JM10961 in the mammal collection of the Queensland Museum.

## BALEEN DESCRIPTION

The baleen of JM10961 is illustrated from the buccal aspect in Fig. 1. There were 282 plates on the right and 280 on the left, a count within the normal range for the species worldwide (Horwood, 1990) and the southern hemisphere in particular (Best, 1985). All-white anterior plates numbered 119 (42%) and 74 (26%) on the right and left respectively. The largest plates measured 27cm in length and 10cm in width. The proportional width of the dark outer border of those plates was 35%. These features, viz. asymmetrical [R>L] anterior white colouration, proportion of all-white plates, length of largest plates and width of the dark outer border, conform with the description by Best (1985) of the dark shoulder (Antarctic) or Type 1 and 2 forms. In contrast, the largest plates of the diminutive (Type 3) form called the dwarf form by Arnold et al. (1987) do not exceed 20cm in length and the plates are either all-white or a large proportion are white.

## SKULL DESCRIPTION

Measurements, after Omura (1975) and Arnold et al. (1987), of the skull, mandible, basihyoid and stylohyals of JM10961 are contained in Table 1 and the structures are illustrated in Figs 2-5. The skulls of three other dark shoulder minke whales considered to be more immature than JM10961, in the Queensland Museum collection, are shown from their dorsal aspects in Fig. 6. Details of those specimens are contained in Table 2. (There are damaged skulls of two other immature dark shoulder forms in the collection as well as intact skulls of two immature dwarf forms.)

Allowing for the immaturity of JM10961, its skull morphology is not appreciably different from the two adult dark shoulder (Antarctic) specimens described by Omura (1975). Exclusion of the parietals from the vertex is evident in JM10961 and the other Queensland dark shoulder forms. The hamular processes of the pterygoids are blunt and rounded (Fig. 7). Omura (1975) considered these two cranial features to be important osteological differences between Antarctic and North Pacific minke whales. In the latter the parietals are included in the vertex, a feature mis-labelled by Horwood (1990: 11), and the hamular processes are elongate, a feature also seen (Fig. 8) in a North Atlantic specimen (D'Alon, 1827).

However, there are some differences between the Queensland dark shoulder specimens and adult Antarctic specimens (Omura, 1975). The anterior concavity of the nasals is less pronounced and this may reflect immaturity but the retro-position of the ascending processes of the maxillaries relative to the nasals and premaxillaries (Figs 2 & 6), a feature of North Pacific specimens (Omura, 1975), may not be explicable



FIG. 1. Baleen from buccal aspect of JM10961. The right baleen row is on the right of the figure.

solely on the basis of immaturity. Whilst further growth of the Queensland dark shoulder whales and those from the North Pacific (which were also immature) may have resulted in maxillary re-positioning, this feature is subject to revision and will require inspection of a larger series of adult specimens from the northern and southern hemispheres. Arnold et al. (1987), however, when describing the features of an adult Type 3 skull from northern Queensland, considered that more immature Type 3 specimens exhibited similar retro-position of the maxillaries. That feature is also evident in the illustration of the skull of an immature 4.1 m long Type 3 specimen (JM8808)

in the Queensland Museum collection (Paterson, 1994).

The supraoccipitals in the Queensland dark shoulder specimens (Figs 2 & 6) differ from Antarctic and North Pacific specimens (Omura, 1975), a North Atlantic specimen illustrated by D'Alton (1827) and Type 3 specimens (Arnold et al., 1987). They are narrow anteriorly, particularly in JM8513, and in JM5434 there is associated depression which may reflect individual variation. The narrowing may be a manifestation of the developing cranium as it is less pronounced in JM10961 which is the most mature of the Queensland dark shoulder specimens.

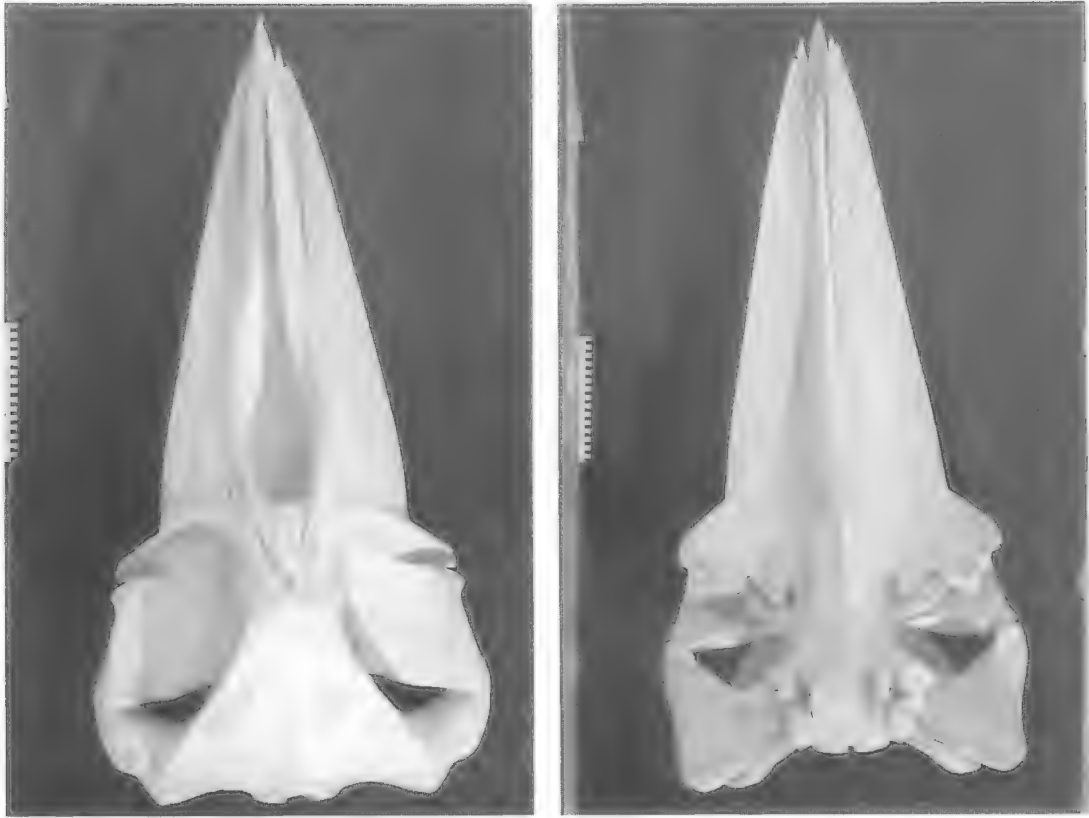


FIG. 2. Skull from dorsal aspect (left) and ventral aspect (right) of JM10961. (Scale in cm)

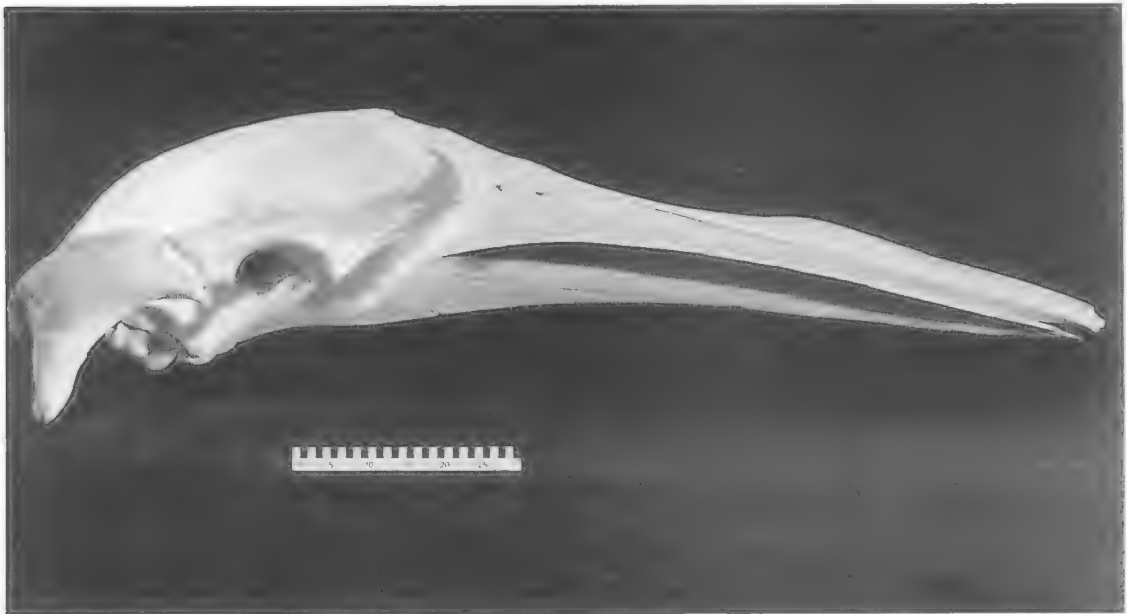


FIG. 3. Skull from lateral aspect of JM10961. (Scale in cm)



FIG. 4. Mandible from dorsal aspect of JM10961. (Scale in cm)



FIG. 5. Basihyoid (below) and stylohyals (above) of JM10961. (Scale in cm)

#### POST CRANIAL DESCRIPTION

**VERTEBRAL COLUMN INCLUDING CHEVRONS.** The vertebral formula (C7, D11, L12, Ca18=48) conforms with the range of 47-50 for the species worldwide and 48-50 from the Antarctic in particular (Ohsumi et al., 1970; Omura, 1957 & 1975; Tomilin, 1967; True, 1904). The caudal region was carefully preserved and dissected and it can be confidently stated that no small caudals were lost. The central epiphyses were unfused with the exception of C1 and Ca 18.

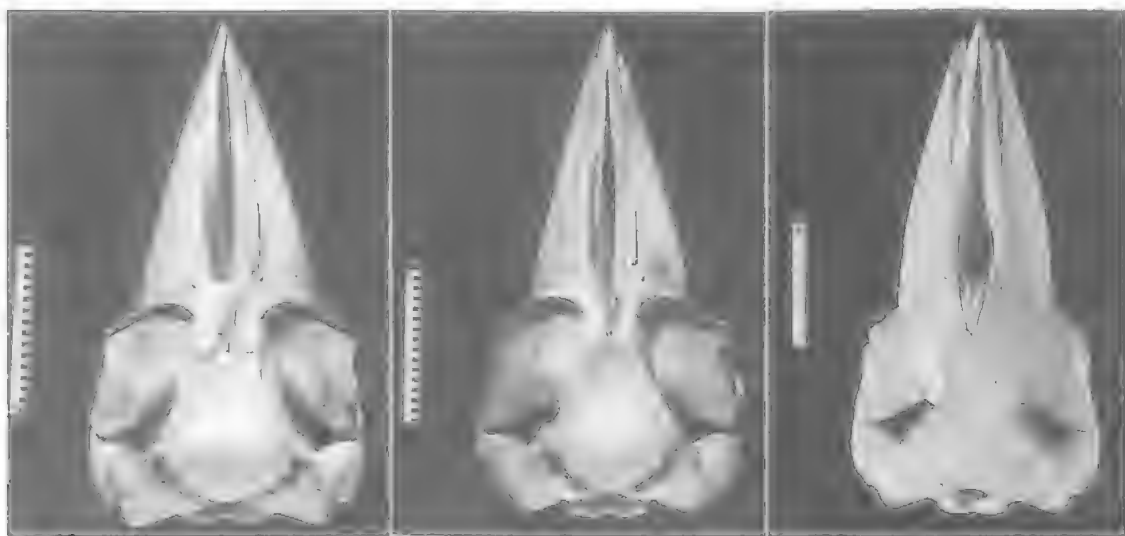


FIG. 6. Skulls from dorsal aspect of J21708 (left); JM5434 (centre); JM8513 (right). (Scales in cm)



FIG. 7. Close-up view of hamular processes of JM10961. (Scale in cm)

The C7 parapophysis is lacking, a feature consistent with other dark shoulder forms (Omura, 1975). The vertebrae are illustrated from their lateral aspects in Fig. 9. Their measurements are contained in Table 3 including mean vertebral length. This value is derived from the formula  $(a \times b \times c)^{1/3}$  where a, b and c represent the breadth, height and length respectively of the centra (Omura, 1971). Comparison between the mean vertebral lengths of two immature North Pacific specimens (5.4 and 6.6 m in length), two adult Antarctic specimens (8.5 and 9.8 m) and JM10961 (6.02 m) is shown in Fig. 10. The values are consistent with the varied maturity of the five specimens.

There were twelve chevrons and they are illustrated in Fig. 11 and their measurements are contained in Table 3. The laminae of the first two and second last were unfused and the last represented by a solitary lamina.

**RIBS AND STERNUM.** There were eleven pairs of ribs and they are illustrated together with the sternum in Fig. 12. Their measurements are contained in Table 4.

**SCAPULAE AND FLIPPER BONES.** The scapulae, humeri, radii and ulnae are illustrated in Fig. 13. The phalangeal formula (including the metacarpals) is I<sub>3-4</sub>, II<sub>8</sub>, III<sub>5-7</sub>, IV<sub>4</sub>, compared with I<sub>4-5</sub>, II<sub>6-8</sub>, III<sub>7-8</sub>, IV<sub>4</sub> from two adult Antarctic specimens (Omura, 1975). Measurements are contained in Table 5.

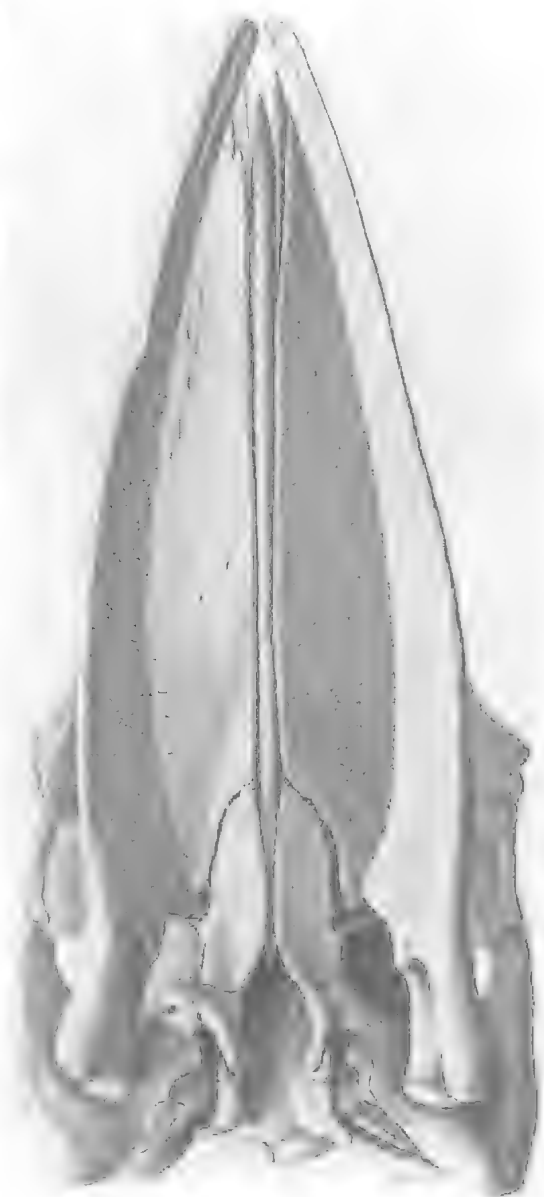


FIG. 8. Skull from ventral aspect of a North Atlantic minke whale (from D'Alton, 1827).

Tomilin (1967) noted that, in northern hemisphere minke whales, the proportional breadth and height of the scapulae increase in larger (older) whales and breadth increases more than height. That observation is confirmed in Table 6 where the relevant scapular dimensions of JM10961 are compared with two adult Antarctic specimens (Omura, 1975).

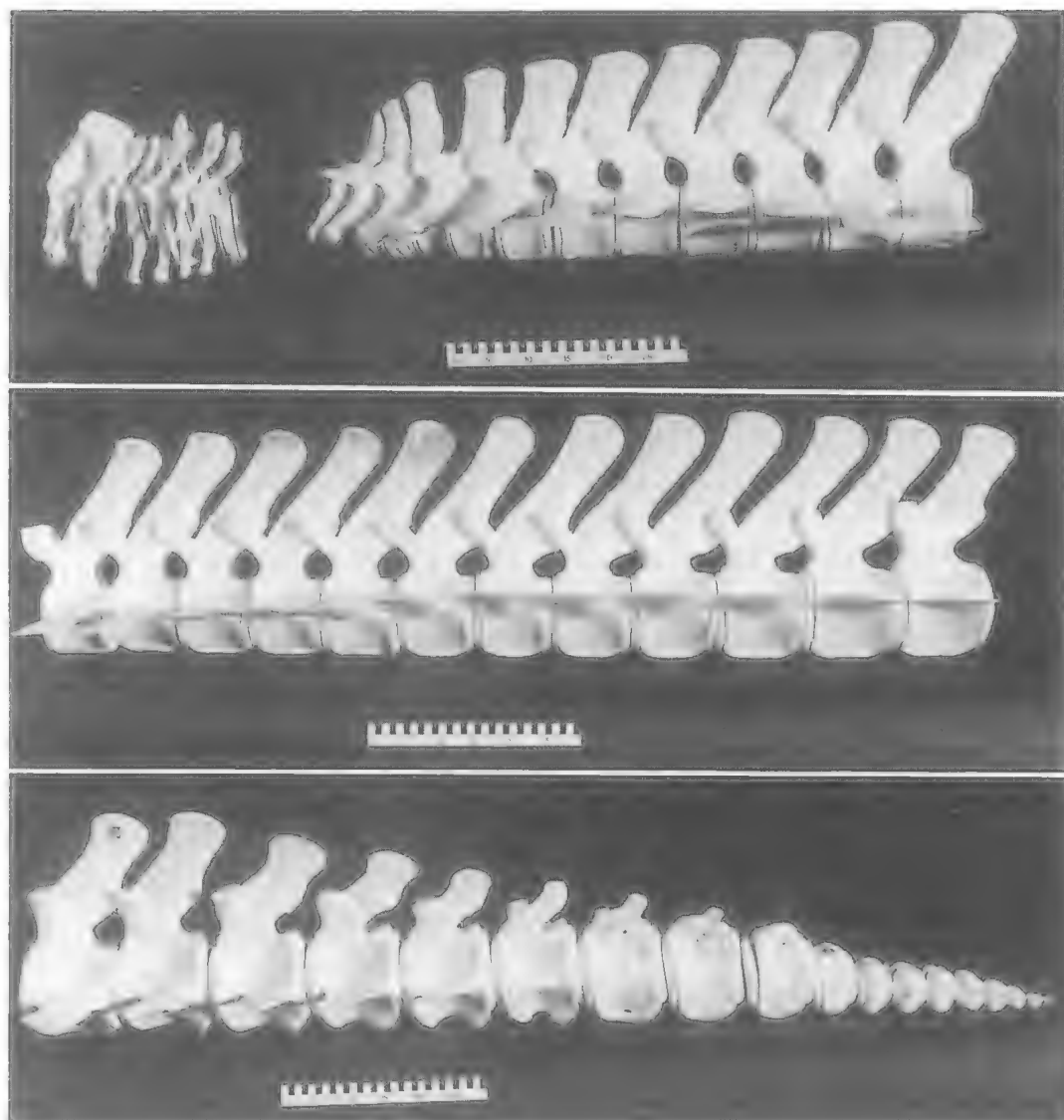


FIG. 9. Vertebral column from lateral aspect of JM10961. Top, cervical and dorsal vertebrae; centre, lumbar vertebrae; bottom, caudal vertebrae. (Scale in cm)

### DISCUSSION

The evidence presented here with regard to the dark shoulder form of minke whale, which is tentatively regarded as *Balaenoptera acutorostrata bonaerensis* (Burmeister, 1867) by Horwood (1990), highlights the problem that the number of specimens available for comparison is limited and they are often immature with resultant difficulties in interpretation of osteological characters. This problem has been considered in detail by Arnold et al. (1987) in relation to the

dwarf (Type 3) form. A future osteological study, in which all adult specimens (particularly those of known Type) in Australasian collections were assessed, may further clarify the taxonomy of *Balaenoptera acutorostrata*.

### ACKNOWLEDGMENTS

Vic Hislop retrieved the whale carcass from the Great Sandy Strait and shore transport was co-ordinated by Geoff Brittingham of the Department of Environment. Paul Avern, Patricia Paterson,

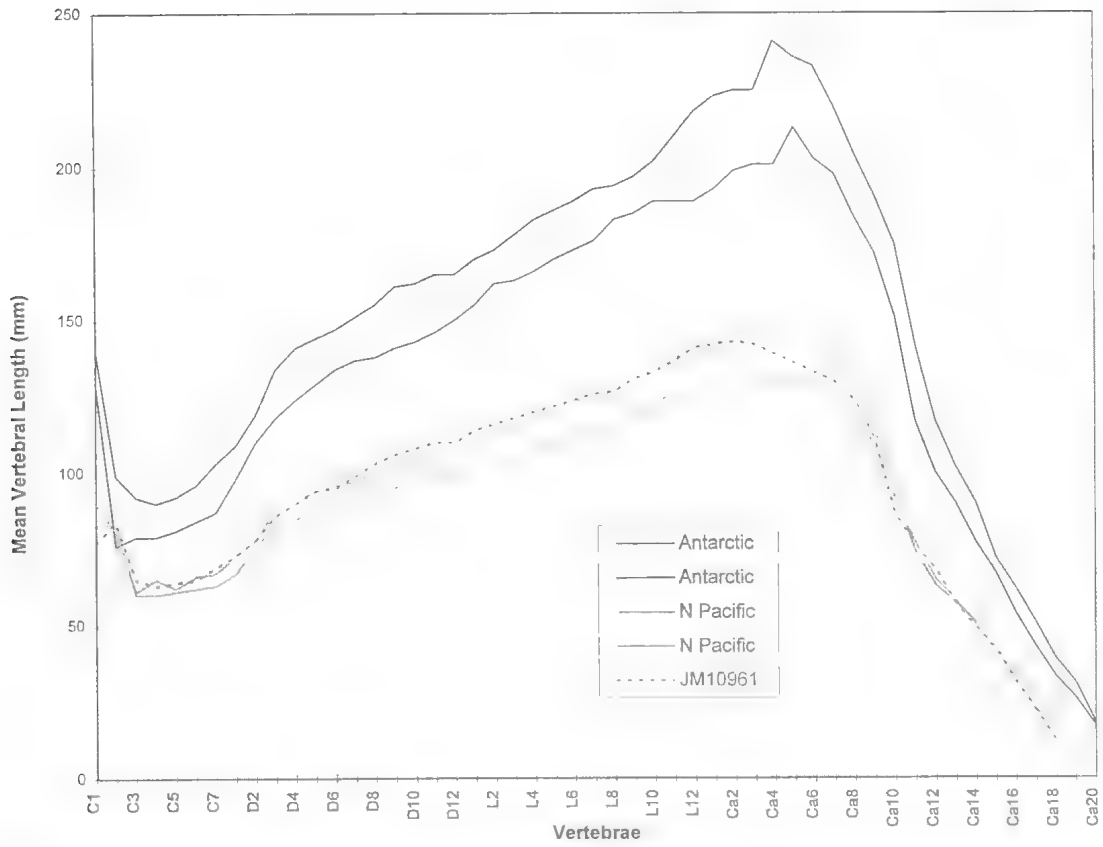


FIG. 10. Comparison between mean vertebral lengths of JM10961, North Pacific and Antarctic minke whales (from Omura, 1975).

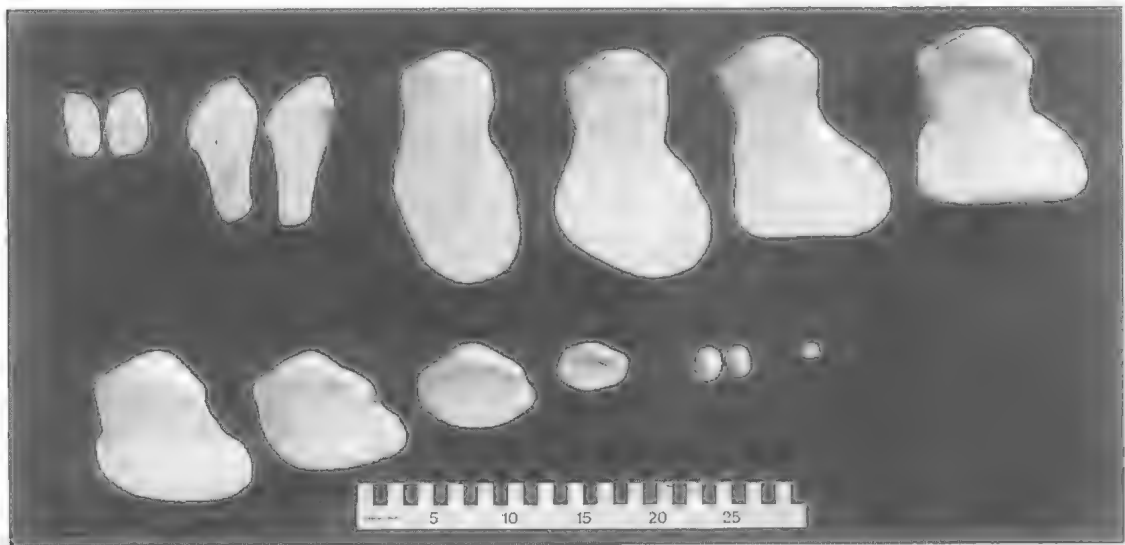


FIG. 11. Chevrons of JM10961. (Proximal at upper left and distal at lower right.) (Scale in cm)



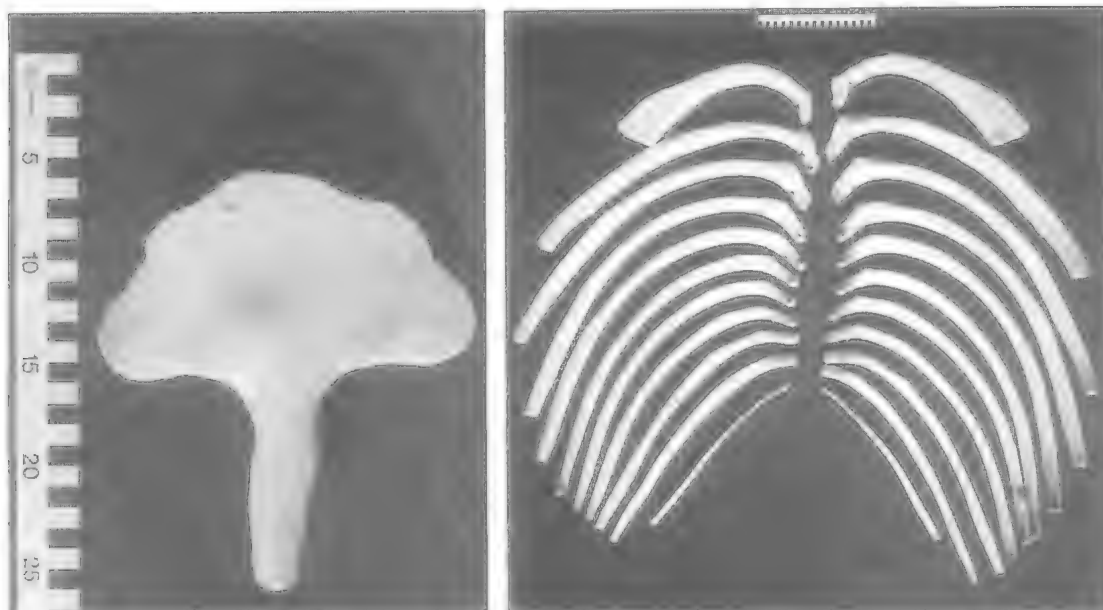


FIG. 12. Sternum (left) and ribs (right) of JM10961. (Scale in cm)

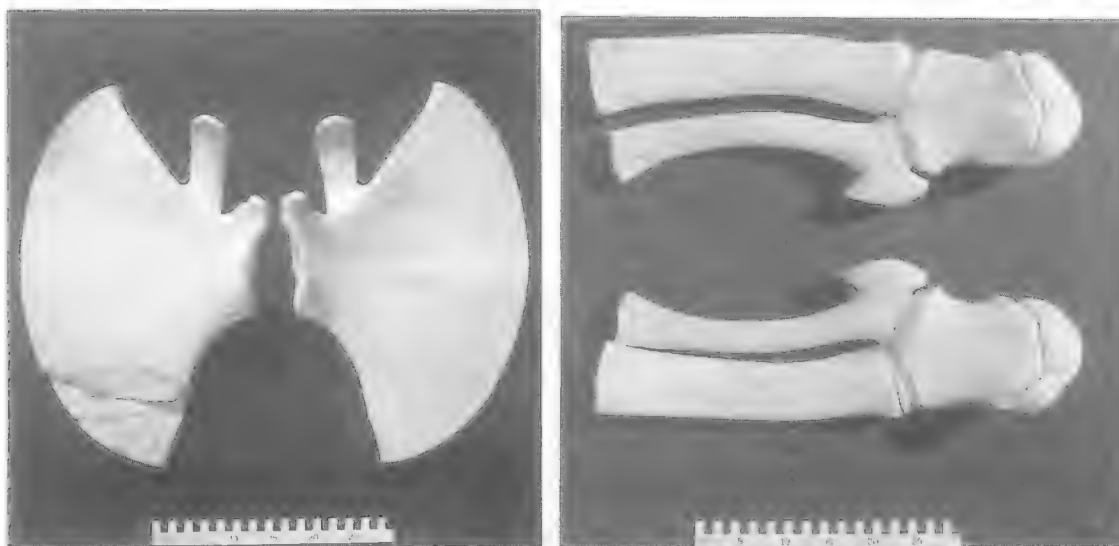


FIG. 13. Scapulae (left); humeri, radii and ulnae (right) of JM10961. (Scale in cm)

Steve Van Dyck and Owen Walker assisted with flensing. Bruce Cowell took the photographs.

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TABLE 1. Skull, mandibular and hyoid measurements (in mm) of JM10961.

Measurement	mm
Condyllo-premaxillary length	1552
Length of premaxillary, right	1053
Length of premaxillary, left	1047
Length of maxillary, superior right	1066
Length of maxillary, superior left	1058
Tip of premaxillary to vertex	1013
Tip of premaxillary to nasals	943
Length of nasals, median	152
Breadth of nasals, anterior (between premaxillaries at anterior end of nasals)	93
Length of rostrum	987
Breadth of rostrum at middle	307
Breadth of rostrum at base	471
Breadth across maxillaries at vertex	162
Breadth of frontal across nasals	167
Breadth between maxillaries at nares	158
Breadth of skull, squamosal	776
Breadth of skull, frontal	670
Breadth of skull, maxillaries	665
Length of orbit, frontal, right	153
Length of orbit, frontal, left	156
Breadth of occipital bone	622
Breadth across occipital condyles (to base of spongy bone)	166
Height of occipital condyle right	113
Height of occipital condyle left	113
Breadth of foramen magnum aperture	75
Height of foramen magnum aperture	64
Length from foramen magnum to vertex (measured at posterior parietals)	423
Tip of premaxillary to anterior vomer, median	144
Tip of premaxillary to anterior palatine, median	950

Measurement	mm	
Tip of premaxillary to posterior palatine, median	1297	
Tip of premaxillary to posterior pterygoid	1507	
Breadth across hamular process of pterygoid	123	
Length of mandible, straight, right	1552	
Length of mandible, straight, left	1532	
Length of mandible, right, outside curve	1652	
inside curve	1610	
Length of mandible, left, outside curve	1653	
inside curve	1615	
Height of mandible at coronoid, right	207	
Height of mandible at coronoid, left	212	
Height of mandible at condyle, right	143	
Height of mandible at condyle, left	145	
Tympanic bulla, length, right	87	
Tympanic bulla, length, left	86	
Tympanic bulla, greatest breadth, right	70	
Tympanic bulla, greatest breadth, left	70	
Tympanic bulla, thickness at middle, right	49	
Tympanic bulla, thickness at middle, left	51	
Malar length, right	188	
Malar length, left	186	
Malar breadth, right	81	
Malar breadth, left	73	
Lachrymal length, right	155	
Lachrymal length, left	150	
Lachrymal breadth, right	68	
Lachrymal breadth, left	72	
Hyoids	Breadth (mm)	Length (mm)
Basihyoid	292	80
Stylohyal, right	42	120
Stylohyal, left	43	121

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TABLE 2. Other dark shoulder minke whales in the Queensland Museum.

Registration No	Sex	Locality	Collection Date	Full Length	Skull Length
J21708	♀	Currimundi, Caloundra, 26°46'S 153°08'E	25 August 1971	-	865mm
JM5434	♀	Granite Bay, Noosa, 26°23'S 153°06'E	5 August 1986	3.84m	930mm
JM8513	♀	Woralie Creek, Fraser Island, 25°08'S 153°06'E	16 November 1990	4.1m	990mm

TABLE 3. Vertebral and chevron measurements (in mm) of JM10961.

Vertebral No.	Greatest Breadth	Greatest Height	Centrum Breadth (a)	Centrum Height (b)	Centrum Length (c)	Mean Vertebral Length (a×b×c) <sup>1/3</sup>
C 1	272	218	193	125	19	77
2	332	188	167	90	40	84
3	296	159	128	90	24	65
4	291	159	122	92	22	63
5	293	186	119	95	23	64
6	300	192	119	97	24	65
7	292	185	121	99	27	69
D 1	293	210	123	98	32	73
2	304	222	115	97	42	78
3	331	243	121	94	56	86
4	375	263	119	94	65	90
5	424	279	120	94	74	94
6	451	286	118	93	78	95
7	459	296	119	94	88	99
8	476	302	129	94	91	103
9	483	301	129	94	97	106
10	497	312	136	95	98	108
11	478	326	137	99	97	110
L 1	473	337	142	102	101	114
2	481	343	145	103	104	116
3	479	347	145	106	107	118
4	480	348	145	108	109	120
5	478	360	146	110	113	122
6	467	370	148	112	114	124
7	456	391	150	114	117	126
8	451	382	151	114	119	127
9	429	390	154	117	124	131
10	415	385	154	119	128	133
11	404	374	156	124	134	137
12	380	358	160	127	139	141

Vertebral No.	Greatest Breadth	Greatest Height	Centrum Breadth (a)	Centrum Height (b)	Centrum Length (c)	Mean Vertebral Length (a×b×c) <sup>1/3</sup>
Ca 1	363	343	159	128	142	142
2	305	344	158	128	144	143
3	291	305	153	128	146	142
4	248	278	151	125	142	139
5	208	246	149	123	138	136
6	163	222	143	122	135	133
7	144	200	143	120	128	130
8	125	175	124	121	127	124
9	112	148	112	123	100	111
10	102	112	101	90	69	86
11	92	88	89	86	57	76
12	83	75	80	74	52	68
13	73	66	63	60	49	57
14	62	57	53	51	45	50
15	54	45	46	41	38	42
16	43	32	34	29	31	31
17	30	23	23	18	25	22
18	18	15	14	11	12	12

Chevron	Length	Height
1	22, 28	43, 44
2	46, 41	94, 99
3	73	151
4	98	151
5	101	134
6	111	116
7	99	100
8	85	77
9	74	60
10	44	35
11	22, 21	17, 16
12	12, -	9, -

TABLE 4. Rib and sternal measurements (in mm) of JM10961.

Rib	Straight Length		Rib	Straight Length	
	Right	Left		Right	Left
1	393	380	7	712	712
2	659	675	8	789	683
3	768	758	9	667	665
4	781	783	10	634	637
5	777	784	11	457	482
6	742	747	Sternum	Breadth 181	Width 195

TABLE 5. Scapular and flipper measurements (in mm) of JM10961.

Scapula			Humerus, Radius, Ulna					
	Right	Left		Breadth		Length		
Greatest breadth	465	466		Right	Left	Right	Left	
Greatest height	257	290	Humerus	109	104	193	190	
Ratio of breadth to height	1.6	1.6	Radius	68	67	347	330	
Length of acromion-inferior	120	113	Ulna	37	37	320	331	
Breadth of acromion, distal end	53	50						
Length of coracoid, inferior	47	45						
Breadth of coracoid, distal end	33	25 *						
Length of glenoid fossa	122	120						
Breadth of glenoid fossa	77	77						
Length of Phalanges								
Phalanx	Right				Left			
	I	II	III	IV	I	II	III	IV
1	52	61	54	42	51	63	53	41
2	47	56	52	34	47	57	52	35
3	36	41	41	29	37	42	42	29
4	17	28	30	21	**	30	30	16
5	-	19	20	-	-	19	21	-
6	-	14	15	-	-	14	**	-
7	-	10	10	-	-	10	**	-
8	-	7	-	-	-	7	-	-
* damaged                      ** possibly missing								

TABLE 6. Comparison between scapulae of adult and immature dark shoulder minke whales (measurements in mm).

Scapula	JM10961				71J2793 (Omura, 1975)				71J2883 (Omura, 1975)			
	Breadth		Height		Breadth		Height		Breadth		Height	
	465	466	287	290	812	805	449	452	874	864	491	491
Condyllo-premaxillary length	1552				2115				2350			
Dimensions as % of condyllo-premaxillary length of skull	30.0	30.0	18.5	18.7	38.4	38.1	21.3	21.4	37.2	36.8	20.9	20.9

**BRYDE'S WHALE *BALAENOPTERA EDENI* ANDERSON, 1878 STRANDED NEAR ROSEDALE, QUEENSLAND IN 1931.** *Memoirs of the Queensland Museum* 42(1): 326, 1997. — Bryde's whale *B. edeni* was the last balaenopterid to be described and its osteological distinction from the sei whale *B. borealis* Lesson, 1828 was not resolved until the studies of Junge (1950) and Omura (1959).

The Queensland Museum Archives contain correspondence between Heber A. Longman, a former Director of the Museum, and Rosedale residents concerning the stranding of a large balaenopterid ~ 6km south of Agnes Water (24°10'S, 151°53'E) in 1931. Longman wrote to Constable E.M. Riley of Rosedale Police Station on 26 November 1931: 'I am greatly indebted to you and Mrs Riley for the information telephoned last week regarding the remains of a whale found near Rosedale. Mr D. Hoare kindly gave me this morning an excellent series of photographs, and it is quite evident that the remains represent a Hump-back Whale, which is technically known as *Megaptera nodosa* ... Although we have a specimen of this whale in the Museum, which was presented by Mr Thomas Welsby, I should very much like to obtain the complete set of bones if they could be secured without much expense'. Riley replied and discussed potential problems associated with possible retrieval — factors no less relevant 65 years later. He recommended that the assistance of Mr F.G. Collins of Rosedale Cattle Station be sought: '... The distance and position where the skeleton [later noted to be ~ 15m long] is situated render it a very difficult undertaking ... It would take about 20 men and 4 or 5 motor lorries to accomplish such a task on a weekend ...'. Riley suggested a possible alternative to road transport viz. that a boat tow, on a very calm day, a log raft on which the bones were loaded to Agnes Water where motor vehicles had ready access to the water's edge. Longman wrote to Collins on 14 December who replied on 29 December making no reference to the water transport proposal: '... One of my men who knows the location well advises that it would be very difficult to convey these large bones from where they are buried in the sand to where it is possible to fit a conveyance to bring them to the nearest Railway Station, a distance not less than 40 miles. There is practically no road from where the whale remains are for about 4 miles and the road from there to Rosedale is mostly bad and rough. I am of the opinion that the expense of recovering these bones and conveying them to the nearest railway would be far too heavy to warrant the outlay ...'. In Longman's hand-writing there is an annotation to the letter: 'Mr Collins visited the Museum on Dec. 31st'. As far as is known the matter rested there — as did the skeleton.

Eleven photographs were sent to Longman. Two are shown here (Fig. 1). It is likely, from the cleanness of the skull and mandible as well as the state of the soft tissues still attached to the post-cranial skeleton [in photographs not shown here], that the whale had been stranded for some months. Its identification by Longman as a large adult balaenopterid is clearly correct but his suggestion that it was a hump-back whale is considered erroneous.

The nasal bones are well demonstrated in the photographs and their anterior margins are concave and inclined forwards on their outer aspects, features seen among balaenopterids in

*B. edeni* and the dark shoulder form of the minke whale *B. acutorostrata* only (Omura, 1959 & 1975). The large size of the skull and mandible of the Rosedale whale excludes *B. acutorostrata*. There are now two specimens of *B. edeni* in the Queensland Museum, J21713 and JM4386, collected from Tin Can Bay and the Great Sandy Strait in 1965 and 1983 respectively. Their diagnostic nasal bone characteristics have been confirmed by Paterson & Van Dyck (1988). The skull of the humpback whale donated by Welsby and referred to by Longman is registered J3343 in the cetacean collection. Its nasals (and those of three other humpback whale specimens more recently collected) are antero-medially peaked and do not resemble the configuration of those of the Rosedale whale or the two *B. edeni* specimens in the Queensland Museum. The anterior nasal margins of the Rosedale whale are well posterior to the posterior maxillary concavity. Junge (1950) considered this an important characteristic of *B. edeni* compared with *B. borealis* in which the anterior nasal margins are at a similar level to the maxillary concavity.

The preserved archival material illustrates perennial problems associated with the retrieval of large cetaceans and has enabled a retrospective identification of *B. edeni*.

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 R.A. Paterson, Queensland Museum, PO Box 3300, South Brisbane, Queensland, Australia 4101; 11 March 1997.



FIG. 1. A, Dorsal view of skull of the Rosedale whale which was estimated to be ~15m in length. The pre-maxillaries are missing and the left maxillary is damaged. B, Skull and mandible.

# RE-EVALUATION OF *EMYDURA LAVARACKORUM*: IDENTIFICATION OF A LIVING FOSSIL

SCOTT THOMSON, ARTHUR WHITE AND ARTHUR GEORGES

Thomson, S.A., White, A. & Georges, A. 1997 06 30: Re-evaluation of *Emydura lavarackorum*: Identification of a living fossil. *Memoirs of the Queensland Museum* 42(1): 327-336. Brisbane. ISSN 0079-8835.

Post-cranial osteological characters can be used to diagnose Australian short-necked chelid turtles to genus. Morphological examination of the Pleistocene fossil *Emydura lavarackorum*, from Riversleigh, shows that it is aligned with the genus *Elseya* not *Emydura* and should be referred to as *Elseya lavarackorum* (White & Archer, 1994). Furthermore, the fossil specimen is not distinguishable from an undescribed extant form of *Elseya* from the Nicholson drainage, with which it shares one unique feature so this name should apply also to this extant form, identified to date only from electrophoretic data. It is Australia's first living fossil turtle, an extant population of a Pleistocene taxon. □ *Chelonia*, *Chelidae*, *Pleistocene*, *fossil*, *turtle*.

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The taxonomy of Australian chelid turtles is poorly known and in dire need of review (Cogger et al., 1983). Recent electrophoretic surveys (Georges & Adams, 1992; 1996) have revealed that in some instances, currently accepted species boundaries are difficult to justify and in others, what are currently regarded as single species are in fact two or more. The detailed morphological analyses required to verify these findings have not been conducted (but see Thomson & Georges, 1996), and until recently it was not possible to distinguish even between extant short-necked genera on the basis of osteological characters (Gaffney, 1977). This paucity of osteological data suitable for distinguishing the extant genera makes the identification of fossil forms, most of which are incomplete specimens, difficult. In many instances, chelid fossils have been assigned to either *Chelodina* or *Emydura*, with little or no evidence presented to eliminate the possibility that the short-necked forms among them may be *Elseya*, *Rheodytes* or *Elusor*.

In 1994 a partial carapace and associated plastron from Riversleigh was described as a new species, *Emydura lavarackorum*, by White & Archer (1994). The fossil specimen was from Terrace Site, a fluvial site on the Gregory River. These authors interpreted the sediments as being Pleistocene in age because of the presence of remains of *Diprotodon optatum* (White & Archer, 1994). The holotype consists of the anterior half of the carapace with some anterior peripherals and an essentially complete plastron

with some pelvic material present. The length of the plastron is 390mm (White & Archer, 1994) which corresponds to a carapace length of approximately 420mm. Two other plastra from the same site were also collected but not described.

White and Archer (1994) assigned the specimen to *Emydura* on the mode of the insertion of the anterior bridge into the ventral surface of the carapace. They found that in the derived state, the anterior bridge is angled steeply backwards towards the rib/gomophosis (called transverse process in White & Archer, 1994), whereas in all other chelids the anterior bridge was found to form a continuous line with the rib/gomophosis.

In this paper, we reassess the generic assignment of the fossil by comparing the fossil material with post-cranial character states we have found useful in separating extant genera of Australian short-necked chelid turtles. We also propose that the fossil taxon is extant, a distinctive, undescribed form closely aligned with *Elseya dentata*.

## MATERIALS AND METHODS

Specimens of each of the short-necked species identified using electrophoresis by Georges and Adams (1996) were obtained from museums, the Conservation Commission of the Northern Territory and the University of Canberra. Where forms have not been included in published keys or descriptions, the specimens were selected from those lodged as vouchers to accompany the elec-

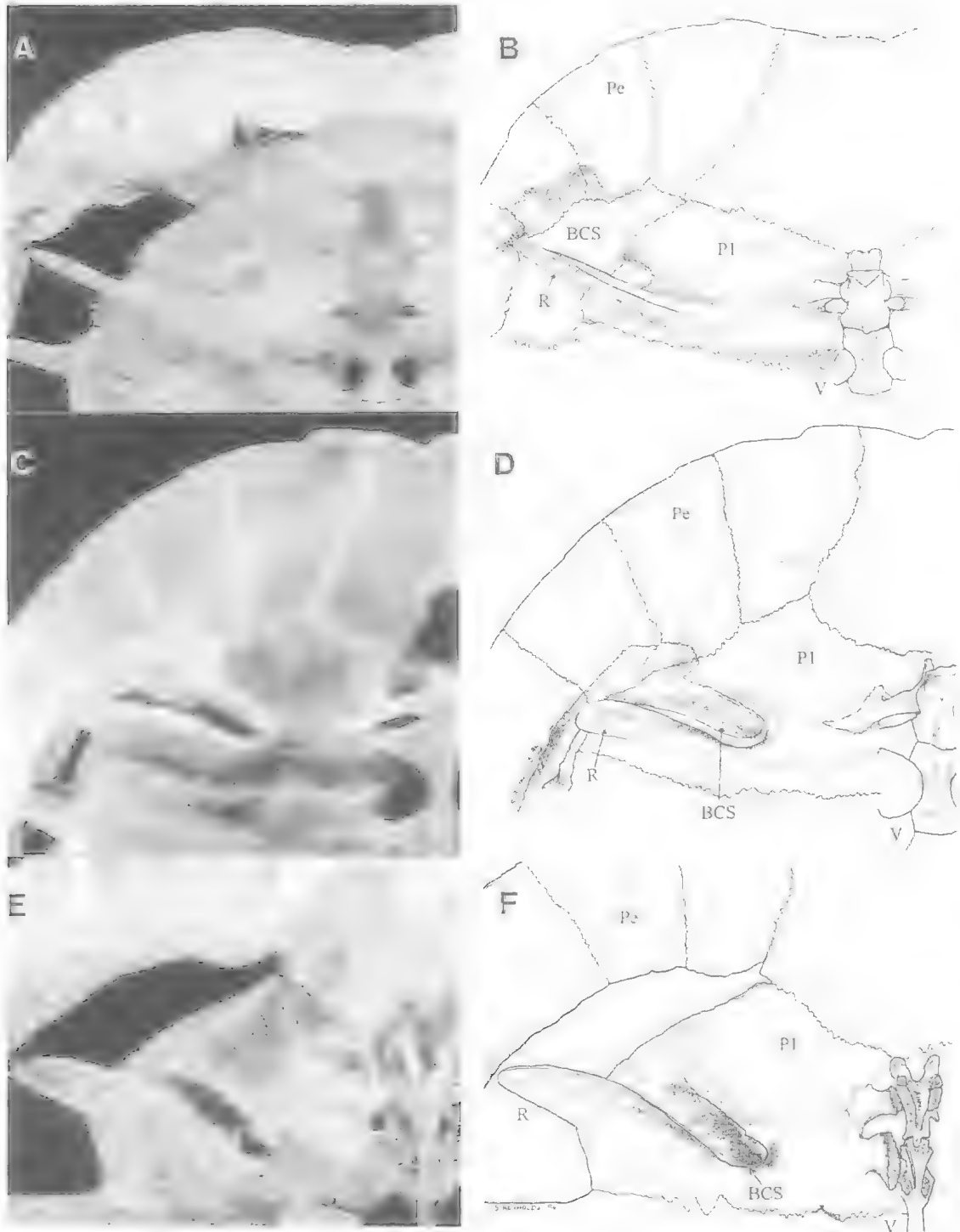


FIG. 1. Ventral view of the anterior carapace of short-necked turtles showing the bridge-carapace suture (BCS) the rib/gomphosis (R) on pleural 1 (Pl) and their relationship to the vertebral column (V) and the peripherals (Pe). A-B, *Pseudemys* (UC0178). C-D *Elseya* sp. aff. *E. latisternum* (Manning) (QM59289); E-F, *Elusormacrius* (UC0184).

trophoretic data. The specimen collection was supplemented by limited field sampling.

Each specimen was skeletonised by removing excess soft tissue and feeding the remaining carcass to dermestid beetles. The skeletal material was bleached in 5% sodium hypochlorite solution, and the process stopped by immersion in 100% ethanol. Plastra were separated from carapaces by disarticulating the plastral-carapacial suture between the hyo- and hypoplastra of the plastron and the lateral peripherals of the carapace. This was done by the carefully heating the carapace until the sutures become mobile and the plastron was then gently prised off. This also required disarticulation of the pelvis from the carapace. Characters potentially diagnostic at the generic level were examined to establish their consistency across a range of specimens within the polytypic genera *Elseya* and *Emydura*, and across a range of specimens within each species.

The fossil specimens of *Emydura lavarackorum* were examined to determine the presence of character states which are generically diagnostic in extant taxa. The fossil specimen was then assigned to genus.

Throughout this paper, we refer to a generic group as a group of species that are sufficiently distinct collectively to warrant recognition at the level of genus, though this has not yet been formally established. These groups were first identified by Legler (1981), have a foundation in electrophoretic studies (Georges & Adams, 1996), and have been referred to since several times in the literature. In contrast, a species complex is a group of species, all but one of which are undescribed, which together presumably represent a distinct clade but which are not considered distinctive enough to warrant recognition at the level of genus.

We refer to the *Elseya dentata* species complex as comprising the distinctive forms of *Elseya* from coastal Queensland currently assigned to *Elseya dentata*, and the Northern Territory forms including *Elseya dentata* (sensu stricto) and *Elseya* sp. aff. *E. dentata* from the Alligator Rivers region (Georges & Adams, 1996). The *Elseya dentata* generic group (sensu Legler, 1981) comprises the *Elseya dentata* species complex plus *Elseya novaeguineae* and *Elseya branderhorsti* from New Guinea. The *Elseya latisternum* generic group comprises *Elseya latisternum* (sensu stricto), a related form from the headwaters of the Darling River drainage and a sibling species pair from coastal New South Wales (Georges & Adams, 1996; Thomson & Georges, 1996). The

later three are currently undescribed. It is not the purpose of this paper to describe new genera, so for consistency, we use the nomenclature of Georges & Adams (1992) and Legler (1981) and recognise six groups of Australian short-necked chelid at generic level: *Elusor*, *Emydura*, *Rheodytes*, *Pseudemydura*, the *Elseya latisternum* generic group and the *Elseya dentata* generic group.

Throughout this paper, names of the bony elements of the shell and the overlying scutes follow those of Zangerl (1969). A complete list of the specimens examined in this study will be found in Appendix A.

## RESULTS

Five characters were identified as diagnostic at generic level. Where polarity is indicated, it was determined by comparison with South American chelids and African pelomedusids in a cladistic analysis (Thomson & Georges, unpublished data). Only those characters relevant to the identification of the fossil specimen are presented.

**ANTERIOR BRIDGE STRUTS.** Character A. Contact with Pleural 1.

A0. In the primitive state, the posterior edge of the bridge-carapace suture runs parallel and adjacent to the rib/gomphosis of pleural 1 (Fig. 1A-F).

A1. In the derived state, the posterior edge of this suture contacts the rib/gomphosis at its anterior end, but is set at a forward divergent angle of between 15 and 50°. This angle is most pronounced in *Emydura*, least in *Rheodytes* (Figs 2A-F, 3A-D).

**Character B. Bridge suture shape.**

B1. The anterior and posterior edges of the bridge-carapace suture diverge from their point of congruence closest to the vertebral column. The widest extent of the suture is distal to the vertebral column and there is no medial constriction (Fig. 1A-F).

B2. The anterior and posterior edges of the bridge-carapace suture are parallel or closely so with a prominent suture surface between them. There is no medial constriction (Figs 2A-B, E-F 3A-B).

B3. The bridge-carapace suture is expanded for its full length, but more so at extremes, there being an obvious medial constriction (Fig. 2B).

B4. The bridge-carapace suture narrows from its widest point proximal to the vertebral column, and constricts completely to form a ridge confluent with the edge formed by the ventral suture of the peripheral bones (Fig. 3C-D).



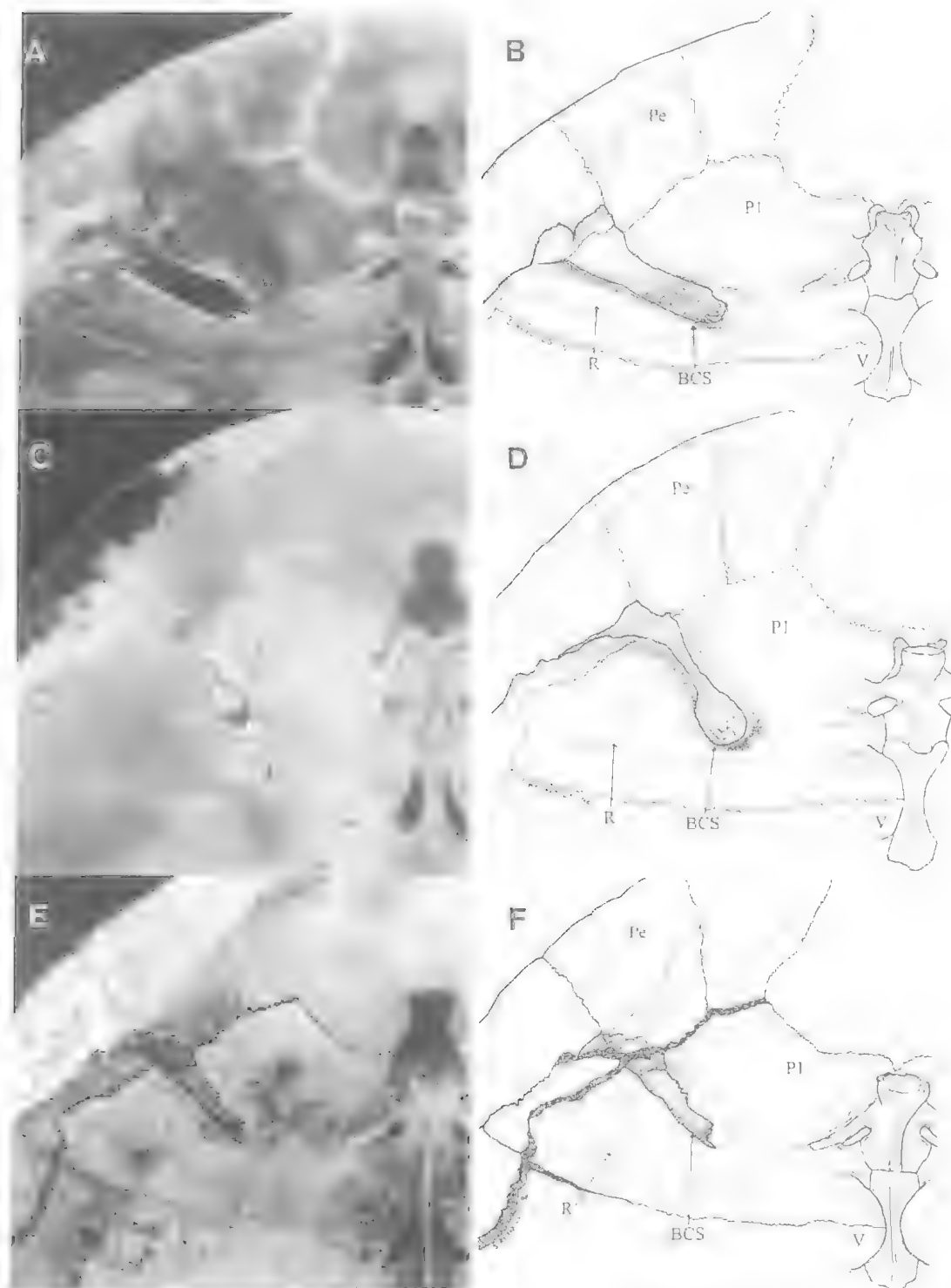


FIG. 2. Ventral view of the anterior carapace of short-necked turtles showing the bridge-carapace suture (BCS) the rib/gomphosis (R) on pleural I (Pl) and their relationship to the vertebral column (V) and the peripherals (Pe). A-B, *Rheodytes leukops* (UC0173). C-D, *Elseya dentata* (QM59277). E-F, *Elseya lavarackorum* (extant) (QM46284).

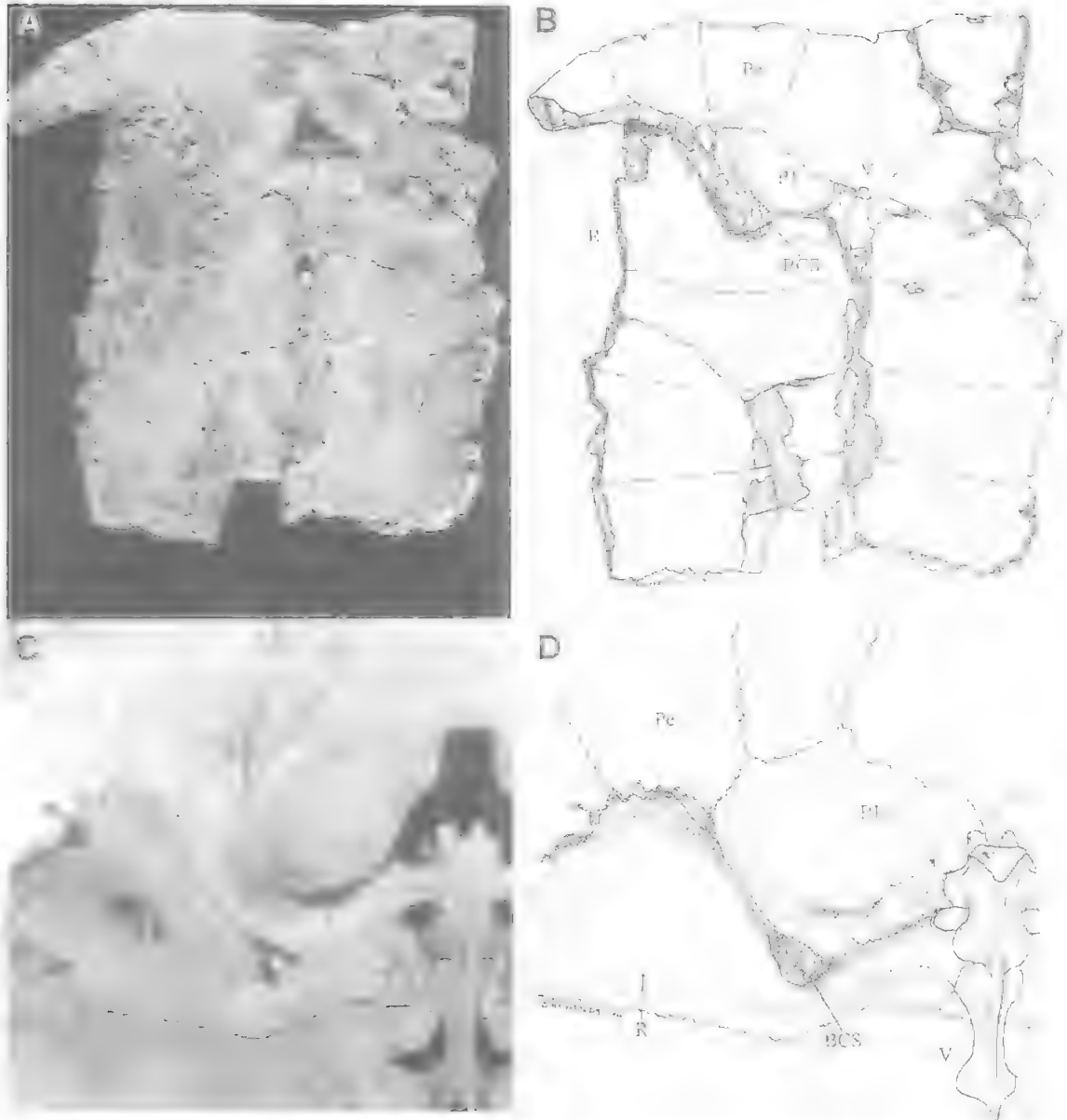


FIG. 3. Ventral view of the anterior carapace of short-necked turtles showing the bridge-carapace suture (BCS) the rib/gomophosis (R) on pleural 1 (Pl) and their relationship to the vertebral column (V) and the peripherals (Pe). A-B, *Elseyia lavarackorum* (fossil) (QM24121). C-D, *Emydura subglobosa* (UC0172).

**RIB/GOMOPHOSIS OF PLEURAL 1.** Character C. Rotation of the Rib/Gomophosis.

C0. The ventral surface of the distal extent of the rib/gomophosis is rotated obliquely, to face ventrally but with posterior inflection (Figs 1A-F, 2A-B).

C1. The rib/gomophosis shows no such torsion distally (Figs 2C-F, 3A-D).

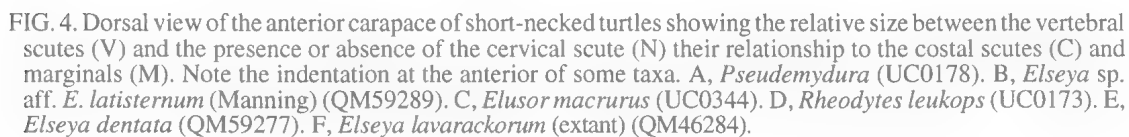
**DORSAL CHARACTERS.** Character D. Relative width of Vertebral 1.

D1. 1st 3 vertebral scutes equal or subequal in width (Figs 4A-D, 5B).

D2. 1st vertebral scute wider than 2nd and 3rd (Figs 4E-F, 5A).

Character E: Cervical Scute.

E0. Cervical scute typically present (Fig. 5B).



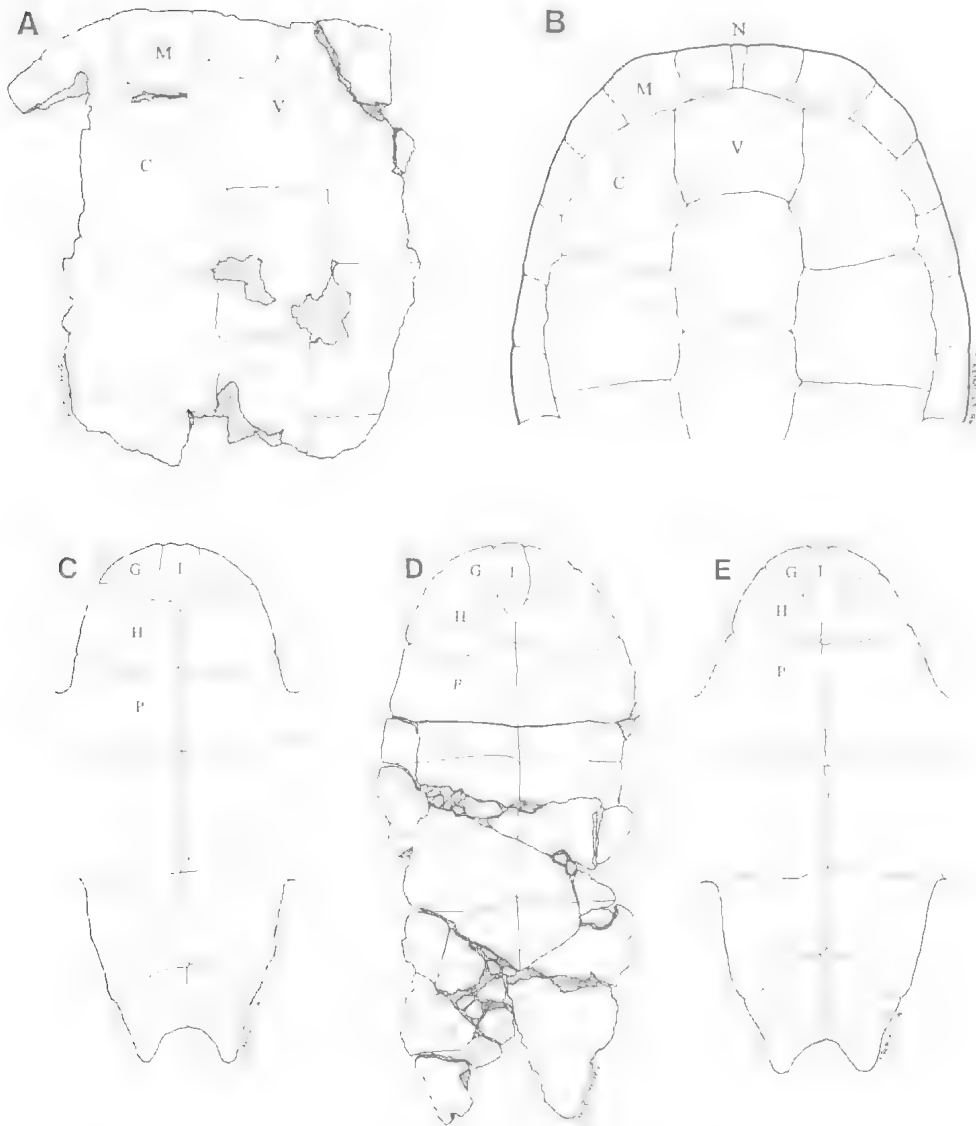


FIG. 5. A-B, Dorsal view of the anterior carapace of short-necked turtles showing the relative size between the vertebral scutes (V) and the presence or absence of the cervical scute (N) their relationship to the costal scutes (C) and marginals (M). Note the indentation at the anterior of some taxa. A, *Elseya lavarackorum* (fossil) (QM24121). B, *Emydura subglobosa* (UC0172). C-E, Ventral view of the plastrons showing the arrangement of the sulci between the humeral (H) and pectoral (P) scutes, also shown are the gular scutes (G) and the intergular (I). C, *Elseya lavarackorum* (extant) (QM46284); D, *Elseya lavarackorum* (fossil) (QM24121). E, *Elseya dentata* (QM59277).

E1. Cervical scute typically absent (Figs 4E-F, 5A).

The distribution of the character states for each taxon is provided in Table 1. The holotype *Emydura lavarackorum* had a combination of a widely divergent angle ( $45^\circ$ ) between the anterior

bridge suture and the rib/gomphosis of pleural one; parallel anterior and posterior edges of the bridge-carapace suture throughout their length, widely spaced, with no medial constriction; no distal rotation of the gomphosis of pleural one;

TABLE 1. Character matrix. Distribution of the key character states among taxa. Abbreviations (s = no. of species examined in group, n = no. of specimens), polymorphic characters shown: Pseud, *Pseudemydura*; Elat, *Elseya latisternum* group; Elus, *Elusor*; Rheo, *Rheodytes*; Else, *Elseya dentata* group; Elns, *Elseya novaeguineae*; EQld, Queensland *Elseya* group; Elav, *Elseya lavarackorum* (holotype); Emyd, *Emydura*.

Taxa	Pseud (s=1) (n=2)	Elat (s=4) (n=20)	Elas (s=1) (n=18)	Rheo (s=1) (n=1)	Else (s=2) (n=25)	Elns (s=1) (n=2)	EQld (s=3) (n=10)	Elav (s=1) (n=1)	Emyd (s=4) (n=25)
Character A	0	0	0	1	1	1	1	1	1
Character B	1	1	1	2	3	3	2	2	4
Character C	0	0	0	0	1	1	1	1	1
Character D	1	1	1	1	2	2	2	2	1
Character E	0	0	0	1	1	0	1	1	0

a first vertebral scute that was markedly wider than vertebrals 2 and 3; and no cervical scute.

A significant feature of *Emydura lavarackorum*, though difficult to quantify, was an indentation of the carapace margin in the area of the cervical cleft and first marginal scutes. This feature is held in common with turtles in the *Elseya latisternum* group and *Pseudemydura*, is variable among the Queensland forms of *Elseya dentata*, and never present in the Northern Territory and New Guinea forms of *Elseya dentata* nor in *Elusor*, *Rheodytes* and *Emydura*. Although not considered a useful character at generic level, we will use it in combination with other similarities to establish a close relationship between the fossil *Emydura lavarackorum* and an extant form of *Elseya* from the Nicholson River.

## DISCUSSION

The bridge carapace suture runs parallel and adjacent to the rib/gomphosis in species of the *Elseya latisternum* group, *Pseudemydura* and *Elusor* and so can be clearly distinguished from the fossil *Emydura lavarackorum* (Table 1). Rotation of the rib/gomphosis of Pleural 1 eliminates *Rheodytes* as a possible identification for the fossil, leaving only the *Elseya dentata* generic group and *Emydura* as possibilities.

Two sub-groups within the *Elseya dentata* generic group can be distinguished. The first comprises *Elseya dentata* (sensu stricto), *Elseya novaeguineae*, *Elseya branderhorstii*, and *Elseya* sp. (Vogelkopf Region, PNG; Anders Rhodin, pers. comm) and *Elseya* sp. (South Alligator River, NT; Georges & Adams, 1996). The second sub-group is restricted to Queensland (Queensland *Elseya dentata* sub-group) and comprises *Elseya* sp. (Nicholson), *Elseya* sp. (Johnstone), and *Elseya* sp. (Burnett) (Georges & Adams, 1996). Generic recognition of these sub-groups is not suggested.

*Emydura lavarackorum* possesses all characters that are consistent across species of the *Elseya dentata* generic group (Table 1) and, more significantly, all characters uniquely possessed by the Queensland *Elseya dentata* sub-group (Table 1). Of those characters which separate *Emydura* from the *Elseya dentata* generic group, the fossil consistently possessed character states which distinguished it from *Emydura*. Therefore, we assign *Emydura lavarackorum* to the genus *Elseya* as *Elseya lavarackorum* (White & Archer, 1994).

Since the description of *Elseya lavarackorum*, specimens of the extant *Elseya* sp. (Nicholson drainage, Georges & Adams, 1996) have become available. The two forms are indistinguishable in every diagnostic character, including the indentation of the anterior margin of the carapace. A unique feature of the Nicholson population, when only extant forms are considered, is the sigmoidal shape of the sulcus between the humerals and pectorals on the plastron (Fig. 5C), this sulcus is straight in all other species of the *Elseya dentata* generic group (Fig. 5E). This feature is present in the holotype of *Elseya lavarackorum* (White & Archer, 1994) and in one (QM30818) of the additional fossil specimens now available (Fig. 5D). The anterior plastron is absent from the third fossil specimen (QM30817).

In contrast, the fossil has strongly embossed, rounded peripherals in the region adjacent to the bridge, a feature not present in the 15 specimens from the Nicholson population. This is a similar condition to that found in aged, adult individuals in a number of species, i.e., individuals which are large for their species, such as *Elusor macrurus* (specimens over 400mm), *Elseya* sp. aff. *E. dentata* from the Burnett River (specimens over 380mm) and *Emydura subglobosa* from the Gregory and Reynolds Rivers (specimens over 250mm). We consider this trait to be essentially a feature of large aged specimens in a range of

chelid turtles. None of the turtles examined from the Nicholson drainage had carapace lengths in excess of 320mm, well below the maximum size for species in the *Elseya dentata* generic group.

In species level taxonomy, the onus is on differential diagnosis. The shell of the fossil holotype is adequately preserved for diagnostic purposes. We therefore propose that, in the absence of any diagnosable difference and the relatively young age of the fossil material, *Elseya lavarackorum* and the Nicholson *Elseya* sp. aff. *E. dentata* be regarded as a single species. It is Australia's first living fossil freshwater turtle, an extant population of a Pleistocene taxon. We do not propose that allochronic subspecies be recognised.

#### ACKNOWLEDGEMENTS

The authors would like to thank Patrick Couper (Queensland Museum), Ross Sadler (Australian Museum), Paul Homer (Museum and Art Galleries of the Northern Territory) and Laurie Smith (Museum of Western Australia) for the loans of fossil and skeletal material and for access to the museum's turtle collections; Peter Whitehead for a large donation of material stored at the Conservation Commission of the Northern Territory; John Cann, John Legler and Gerald Kuchling for the loan of material from their private collections and the Department of Environment and Heritage in Queensland for permits to collect in the Nicholson Drainage of north west Queensland. We would especially like to thank Simone Reynolds of the University of Canberra for the illustrations in this paper and Peter Ogilvie for the photography.

#### APPENDIX A

**Specimens Examined:** All names used for undescribed species are from Georges & Adams (1992, 1996). Abbreviations used: AM, Australian Museum; NTM, Museum and Art Galleries of the Northern Territory; QM, Queensland Museum; WAM, Western Australian Museum; UC, University of Canberra; UM, University of Michigan Field Series; UU, University of Utah.

*Elusor macrurus*: UC0184-93, 0225-29, 0344, UU19488, 19508; *Elseya dentata*: NTM13319, 13521, 16330, QM59265, 59277-80, UC0307-18; *Elseya latisternum*: AM123037, 123039, 125474-75, QM48054-55; *Elseya novaeguineae*: AM42662, 125038; *Elseya lavarackorum*: QMF24121, F30817-18 (fossil), QM31939, 31942, 31944, 31946-47, 31949-50, 31952, 46284, 47908, 47911, 48544, 48547, 60255, UC0201 (extant); *Emydura macquartii*: QM48016, 48034, 48050-51, 59275-76, UC0175-76,

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- 0303; *Emydura subglobosa*: NTM5028, 8206, 13428, 13433, 16332, UC0171-72, 0177; *Emydura victoriana*: NTM13513-14, 32917, 32976, UC 0165; *Elseya* sp. aff. *E. dentata* (Burnett): UC 0305-6, QM2966, 28449, 36036, 36039, 36041-42, 36044-47, 37933, 38533, 59269-71; *Elseya* sp. aff. *E. dentata* (Johnstone): QM22694, 23175, 23299, 23300, 23322, 24938, 28449, 48060, 48068; *Elseya* sp. aff. *E. dentata* (South Alligator): AM128002, 128004, QM59285-89, NTM5097, 13512, 13985, UC0304; *Elseya* sp. aff. *E. latisternum* (Gwyder): AM123028-29, QM 48028, 48038; *Elseya* sp. aff. *E. latisternum* (Bellingen): AM138387-88, UM02016-17; *Elseya* sp. aff. *E. latisternum* (Manning): AM123040, 123042, QM-59289-90; *Emydura* sp. aff. *E. victoriana* (Daly Mission): AM125470-71, 125491, NTM8211, 8213, 17339; *Pseudemydura umbrina*: UC0178, WAM29337; *Rheodytes leukops*: UC0173.

XEROMYS MYOIDES THOMAS, 1889 (RODENTIA: MURIDAE) IN MANGROVE COMMUNITIES OF NORTH STRADBROKE ISLAND, SOUTHEAST QUEENSLAND

STEVE VAN DYCK

Van Dyck, S. 1996 06 30: *Xeromys myoides* Thomas, 1889 (Rodentia: Muridae) in mangrove communities of North Stradbroke Island, southeast Queensland. *Memoirs of the Queensland Museum* 42(1): 337-366. Brisbane. ISSN 0079-8835.

Seven mangrove communities spanning the north-south length of western North Stradbroke Island were surveyed between 1991 and 1993 for *Xeromys myoides*. It was recorded at all sites, a total of 111 individuals was captured and home range estimates and ecological data were recorded for nine individuals. The life history of this small, spotted, specialised, non-aquatic, non-arboreal, nocturnal rodent revolved around the island's mangrove and adjacent sedgeland communities. It nested in either large termitarium-like mounds or simple tunnels in the supralittoral bank. Nests contained up to eight individuals of all age groups and either sex, with one adult male present in the resident group. From their nests, rats followed the receding tide out through sedgeland and into the mangroves where they foraged over a home range estimated at approximately 0.8ha for males and 0.6ha for females. Home ranges overlapped slightly, but core areas, estimated at around 0.2ha, did not. Home range size was thought to be determined by the complexity of the mangrove community as reflected in the structural diversity of the mangrove substrate. The diet of *X. myoides* consisted of small crustaceans (mainly the crabs *Parasesarma erythrodactyla* and *Helice leachi*), marine polychaetes, marine pulmonates and marine bivalves. The species was recorded in breeding condition throughout most of the year. It is proposed that the unusual life-style of this rodent might be linked to problems associated with the need to dissipate heat rather than the necessity to retain it. Caution should be exercised in attributing its locally abundant status on North Stradbroke Island to populations on the mainland which await assessment. □ *Xeromys*, False Water-rat, rodents, mangroves, North Stradbroke Island.

Steve Van Dyck, Queensland Museum, P.O. Box 3300, South Brisbane, Queensland 4101, Australia; 20 December 1996.

The False Water-rat *Xeromys myoides* Thomas, 1889 (Fig. 1) is a small, poorly known Australian hydromyine rodent. Fourteen museum specimens are known (Van Dyck & Durbidge, 1992). These and other specimens liberated after capture, have been collected from mangrove forests, freshwater lagoons, swamps or sedged lakes close to foredunes in the Northern Territory (Parker, 1973; Redhead & McKean, 1975; Magnusson et al., 1976), coastal central Queensland (Thomas, 1889; McDougall, 1944) and coastal southeast Queensland (Dwyer et al., 1979; Van Dyck et al., 1979). It is not known whether the paucity of this record reflects genuine rarity or the inadequacy of searching effort in the appropriate habitat, however the animal is currently classified under the Commonwealth Endangered Species Protection Act 1992 as 'vulnerable'.

*Xeromys myoides* has been known from North Stradbroke Island, Queensland since 1978 when an adult female was hand-caught by students at Myora Springs (Van Dyck et al., 1979). This specimen represented the most southerly record for the species. In 1992, Ellie Durbidge and I recorded the capture of another adult female

trapped near one of a number of reed-covered peat mounds in sedgelands of the Myora wetlands (Van Dyck, 1992, 1994; Van Dyck & Durbidge, 1992). These reports commented on the similarity of the large, termitarium-like nesting mounds to that described by Magnusson et al. (1976) from Melville Island but, in addition, noted the presence of relatively simple tunnels built into the supralittoral bank at the marine-sedgeland/freshwater-wallum (*Banksia* tree-heath on humus podzols) ecotone. In tentatively attributing these simple tunnels to *X. myoides* the possibility was raised that the absence of large nesting mounds in appropriate habitat may not be a reliable gross indicator of the absence of *X. myoides*.

In an attempt to clarify the distribution of *X. myoides* in the mangrove communities of North Stradbroke Island, nest recording and trapping surveys were conducted from near Amity on the island's north-westerly tip, to Jumpinpin, the island's southern extremity 36km south (Figs 2-6). Radiotelemetry of animals trapped and released was expected to generate some preliminary information for the species on diet,



FIG. 1. *Xeromys myoides*, adult female from Rainbow Channel, North Stradbroke Island (Bruce Cowell).

home range, foraging behaviour and aquatic adaptation.

#### METHODS

**FIELD SURVEYS.** Field observations and surveys associated with this study were made between 3 Nov 1991 and 18 Nov 1993. Fieldwork prior to Sept 1992 concentrated on nest appraisal, capture and radiotelemetry of individuals at and near the Rainbow Channel (site 2, Fig. 3), while the latter part documented the presence of *X. myoides* in six other areas of mangrove habitat along the western side of the island (Figs 2-6).

**CAPTURE TECHNIQUES.** Elliott (Elliott Scientific, Upwey, Victoria) size A aluminium traps (300x100x90mm) were used. Up until Sept 1992 trapping was conducted only at or near nesting mounds, none of which was found constructed inside the mangrove zone but in sedges of the supralittoral zone. Thereafter, given the initial results of direct observation through radiotelemetry, traps were laid along the floor of the mangrove forest. A white cotton string-line guide was laid simultaneously. Traps, baited with

chunks of chopped mullet or gar, were placed among mangrove roots, beside trunks with base hollows, among pneumatophores or inside hollow logs. Traps were not set up in trees.

Normal terrestrial trapping protocol was adjusted to accommodate threats of drowning implicit in the method. Live-trapping on the mangrove floor required local knowledge of both the upper inundation height of night high tides and the rates of incoming tides as traps required checking and tripping prior to their inundation. A rising tide combined with too many traps set over a long mangrove transect (e.g., 75 traps over 1km) proved a drowning hazard to trapped rats and a formidable task for one person in a night. Looping of mangrove traplines (25 traps per loop) north and south of a 'central' land-based camp gave adequate coverage of mangrove forest, and quicker access to both traps and the station associated with processing captures. Trapping was carried out during the following periods: Nov 1991 (8 trap nights); Feb 1992 (13 trap nights); May 1992 (249 trap nights); June 1992 (29 trap nights); July 1992 (196 trap nights); August 1992 (188 trap nights); September 1992 (263 trap nights); October 1992 (50 trap nights); November



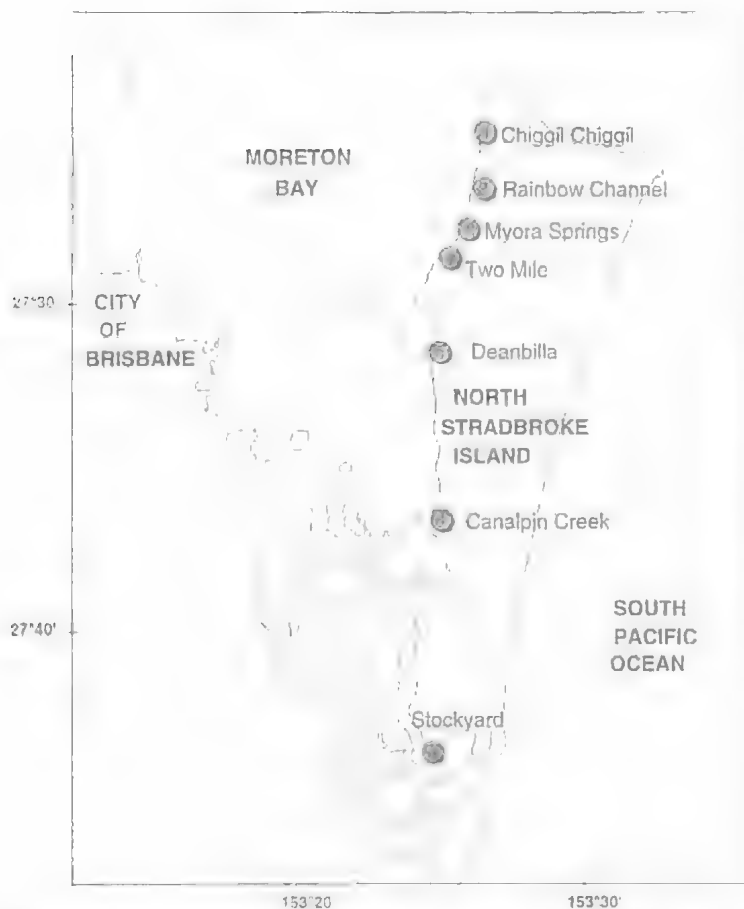


FIG. 2. Sites (1-7) surveyed for *Xeromys myoides* on North Stradbroke Island.

1992 (50 trap nights); December 1992 (100 trap nights); Jan 1993 (50 trap nights); March 1993 (70 trap nights); May 1993 (50 trap nights); July 1993 (40 trap nights); October 1993 (40 trap nights); November 1993 (36 trap nights). Trap nights totalled 1480 and covered sites at Chiggil Chiggil, Rainbow Channel, Myora Springs, Two Mile, Deanbilla, Canalpin Ck and Stockyard (see Table 1, Figs 2-6).

In open *Avicennia marina* woodland such as at Canalpin Creek, where old trees were widely spaced and the substrate simple, it was possible to spotlight for *X. myoides* among pneumatophores and capture them by hand.

No attempt was made to dig individuals from nests and no nesting mounds were breached.

**HANDLING AND RADIO-TRACKING PROCEDURES.** Captured individuals were weighed, measured, sexed, and assessed for reproductive

condition and individual traits (tail kinks, albinism in tail-tip, ear damage etc.). Initial difficulty in determining sex in juveniles and sub-adults was resolved using a measure of the distance between the anus and the urogenital opening ('anal-genital distance') which was significantly less in females (Table 2). *X. myoides* rarely struggled, and gave the impression of being almost incapacitated by fear. However, when handled with ungloved hands they inflicted deep bites, so were restrained for measuring through a cloth collecting bag rolled back to give access to the animals. Dorsal spotting patterns were recorded (Table 2), and each animal was assigned to an age category by weight: J (juvenile) <28g; SA (sub-adult) 28-35g; A (adult) >35g. Each animal was individually tagged. Initially, animals were tagged on one ear with a numbered brass tag (Hauptner-Ohrmarken #73850) or a 'fish & small mammal tag' (No. 1005-1, size 1, National Band and Tag Co, Newport, KY). Both tag types proved unsatisfactory and were found to have been ripped from ears after a

few days. Finally, a system of ear nicks was used. A simple 2mm cut was made in the edge of the pinna with small surgical scissors dipped in tattoo ink. Using well-defined areas of the upper and lower folds of the pinnae, a wide range of identificatory combinations was available. Ear cuts healed and rejoined quickly, leaving a fine black line readily discernable when torch-illuminated from behind the pinna.

Trapped animals were measured (Table 2) and released before dawn at their point of capture, or their nest (where known). In cases where a nest site was not known for an individual and the incoming tide had covered the capture site, the animal was deposited nearest the trap site in a low mangrove hollow that provided cover and easy access to the ground. Animals responded passively but poorly to being held over for measurement during the day following their capture, and

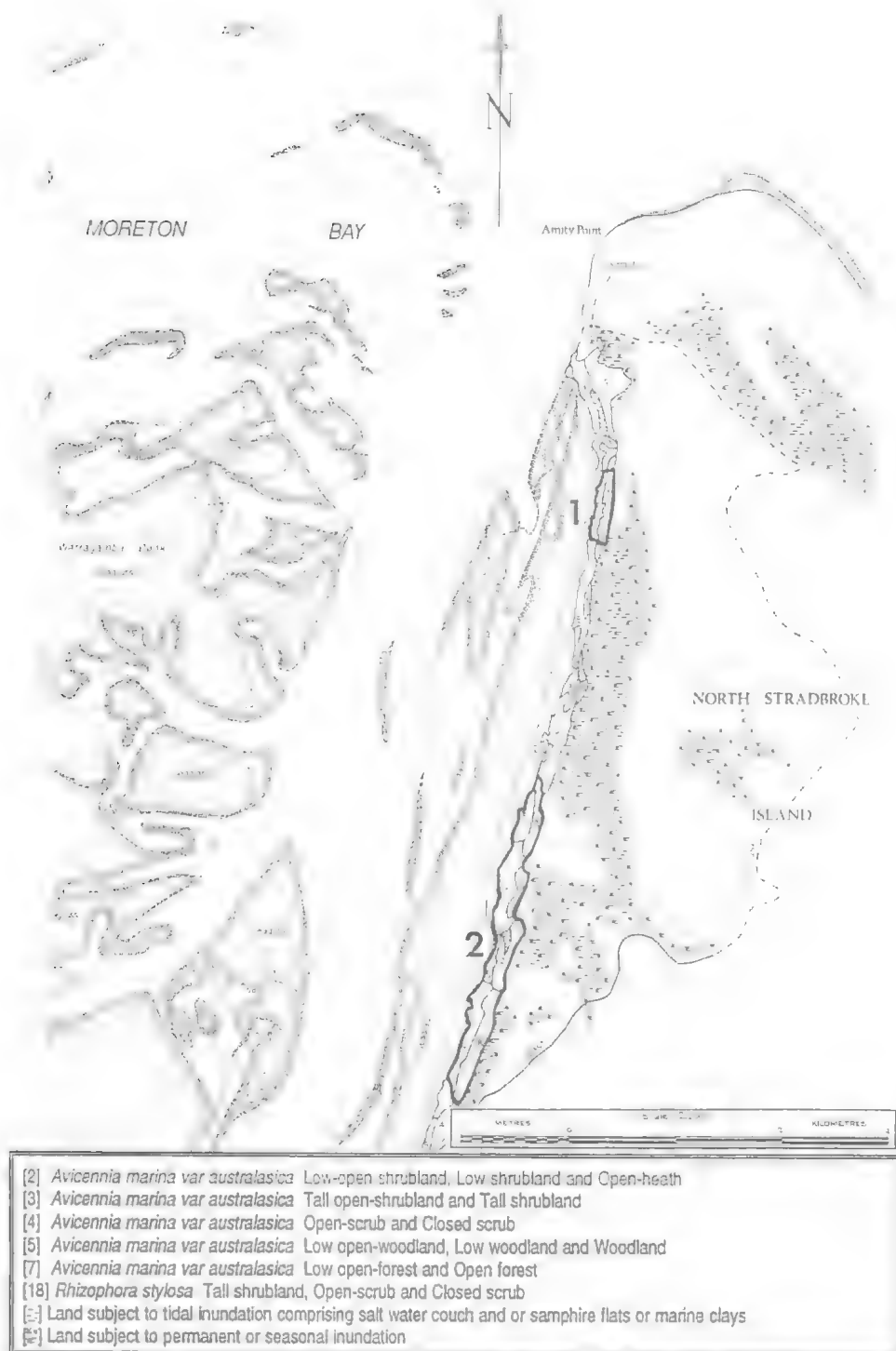


FIG. 3. Sites and vegetation types surveyed for *Xeromys myoides* on North Stradbroke Island at (1) Chiggil Chiggil and (2) Rainbow Channel (after Dowling, 1986).

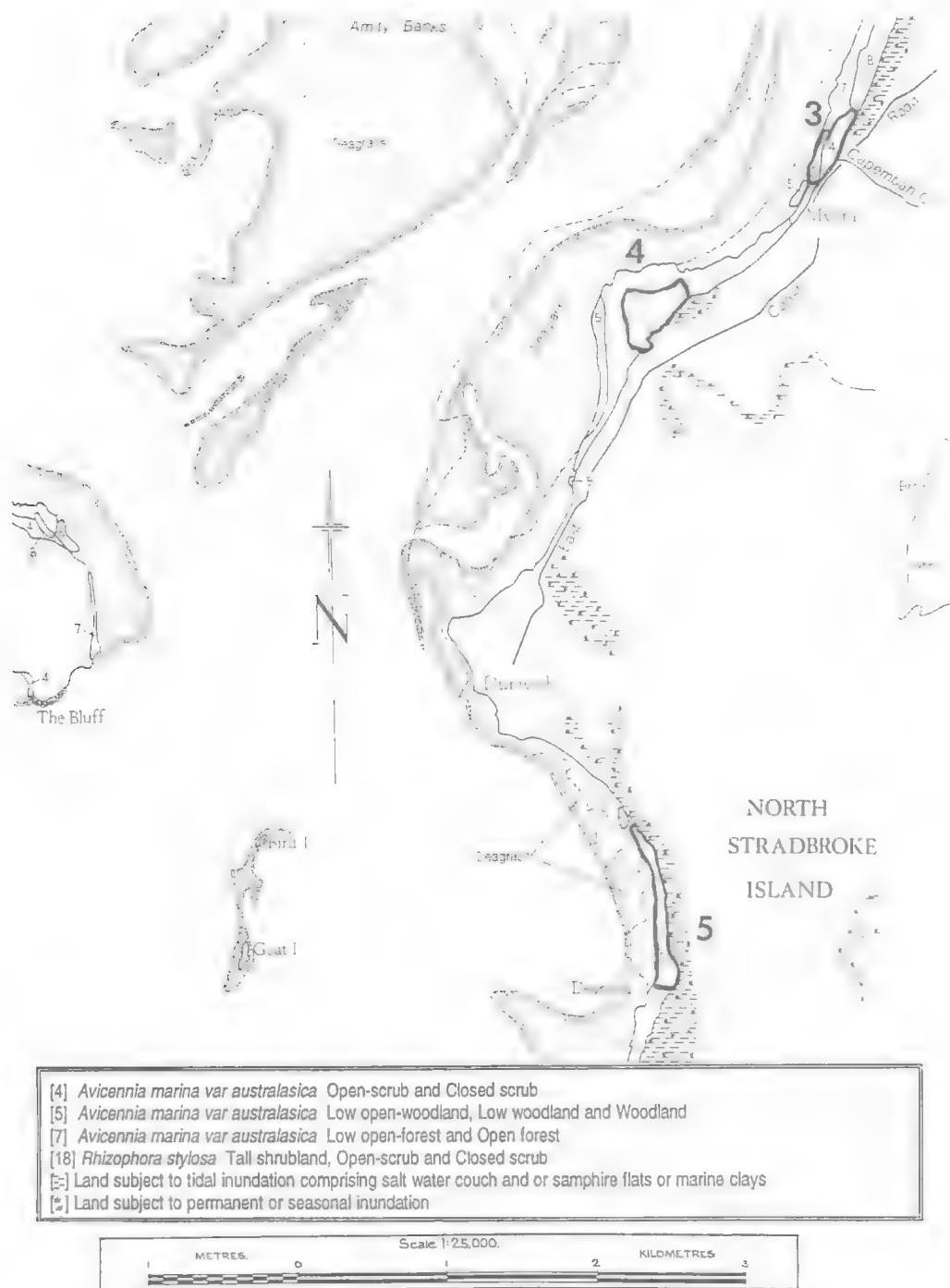


FIG. 4. Sites and vegetation types surveyed for *Xeromyrmex myoides* on North Stradbroke Island at (3) Myora Springs, (4) Two Mile and (5) Deanbilla (after Dowling, 1986).

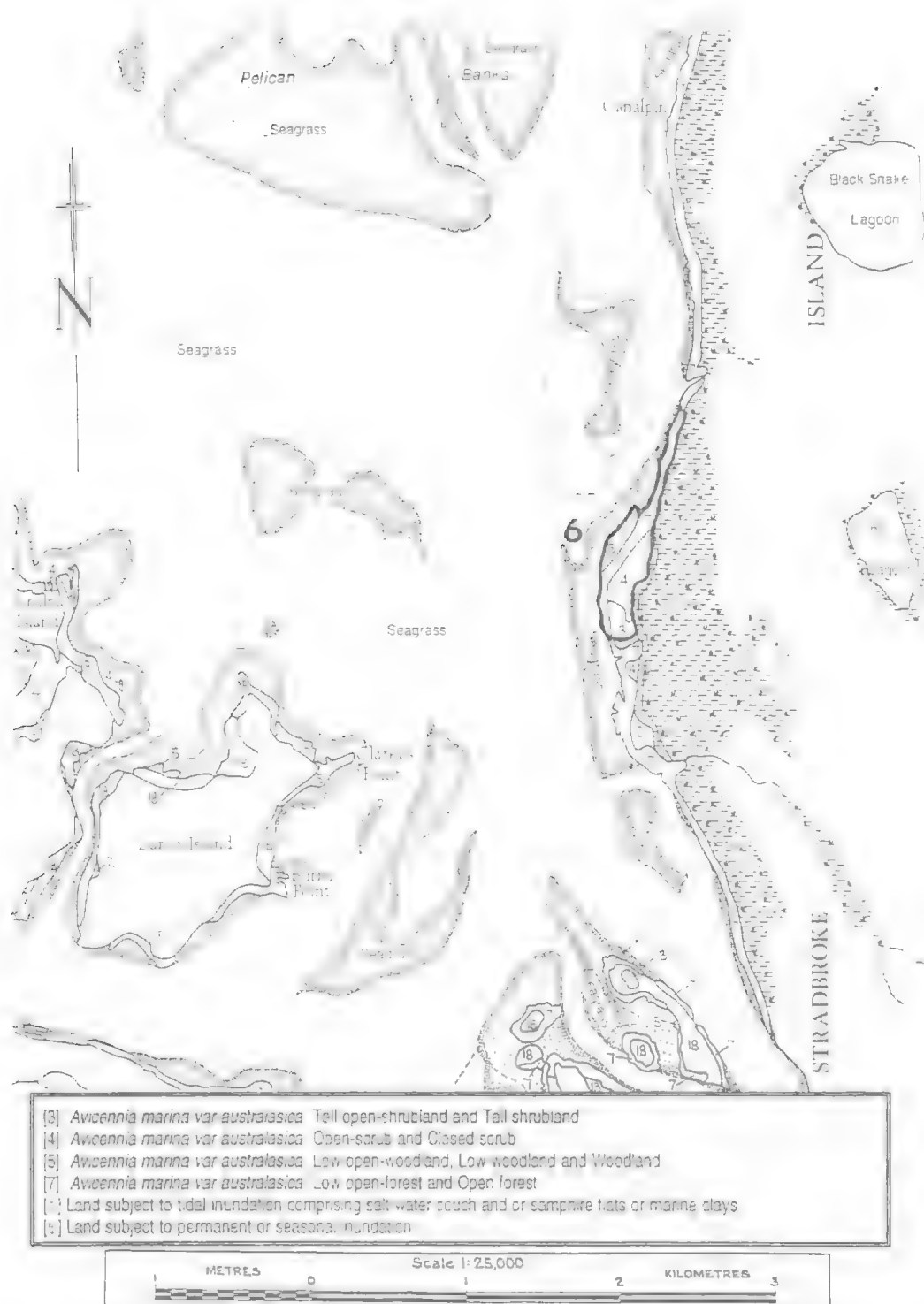


FIG. 5. Sites and vegetation types surveyed for *Xeromys myoides* on North Stradbroke Island at (6) Canalpin CK (after Dowling, 1986).

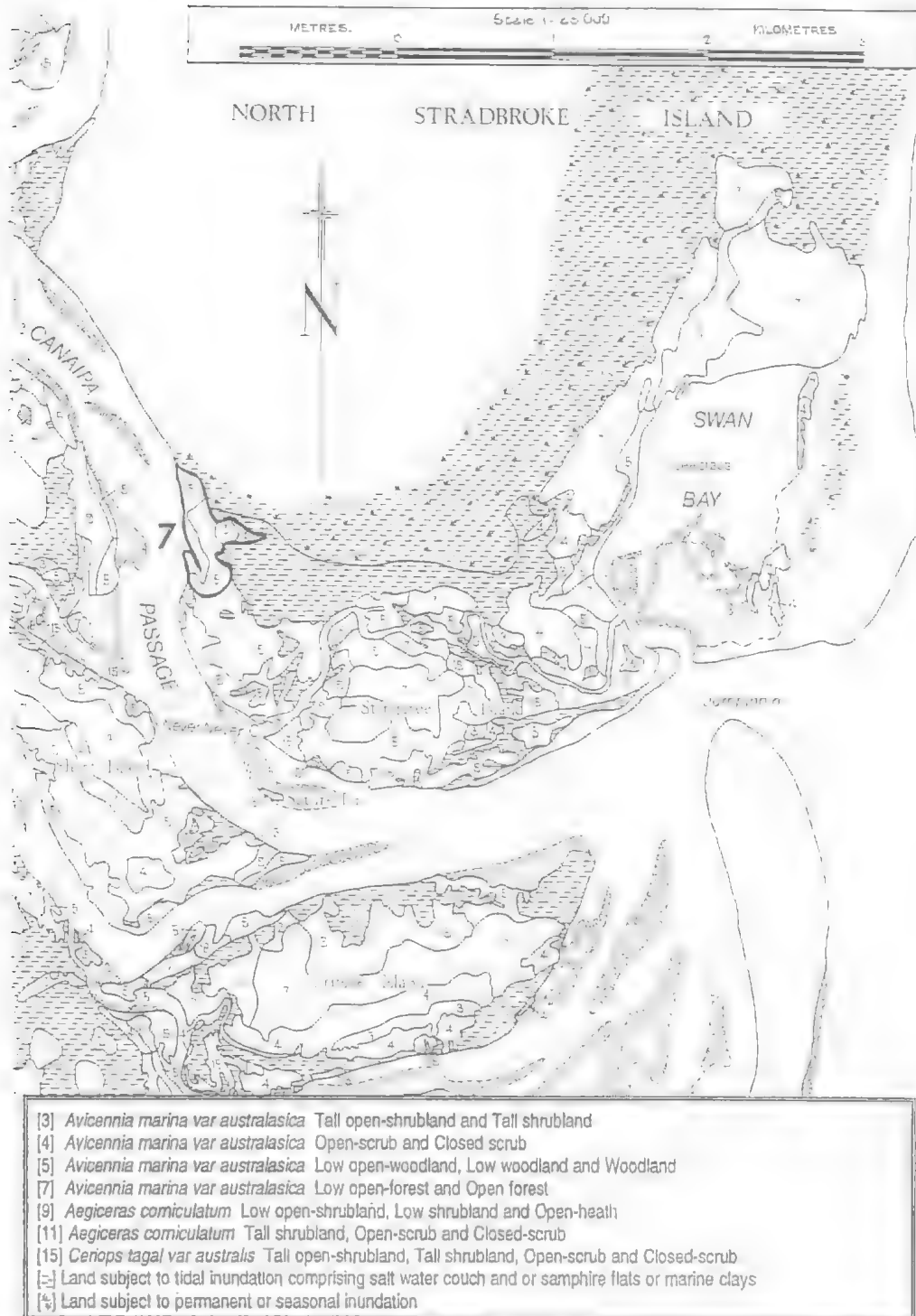


FIG. 6. Sites and vegetation types surveyed for *Xeromys myoides* on North Stradbroke Island at (7) Stockyard (after Dowling, 1986).

TABLE 1. North Stradbroke Island sites surveyed, vegetation types and trapping results for *Xeromys myoides*.

Site	Latitude/Longitude block	Vegetation type(s)	Trap Nights	Captures	Recaptures	Individuals
1 Chiggil Chiggil	27°25'00-10"S 153°26'13-19"E	3,5	64	8	1	7
2 Rainbow Channel	27°27'06"-28°00"S 153°25'22-49"E	2,3,5,7,18	1153	128	48	80
3 Myora Springs	27°28'10-21"S 153°25'18-26"E	4,5	25	6	0	6
4 Two Mile	27°28'43-53"S 153°24'31-49"E	7	25	1	0	1
5 Deanbilla	27°30'48"-31°09"S 153°24'41-47"E	5	45	8	1	7
6 Canalpin Ck	27°36'08-44"S 153°24'22-42"E	3,4,5,7	70	6	0	6
7 Stockyard	27°43'28-46"S 153°24'17-30"E	4,5,9,15	50	5	1	4
Totals			1432	162	51	111

in some cases behaved in an ataxic manner when released the following evening. Rats used in radio tracking were fitted with a Titley (Ballina, NSW) 'Microlite', two-stage transmitter either attached to a cable-tie collar with a protruding 15cm whip antenna or epoxy-potted into a small rectangular tablet (length 17.7mm, breadth 9.3mm, height 6.8mm) with a protruding 18.5cm antenna. The ventral surface of the epoxy disc transmitter was glued to a 20mm x 10mm piece of cloth which was in turn glued to the animal's rump (Selley's Supa Glue) after a square of fur approximating the dimensions of the cloth had first been cropped close to the rat's skin. The short hair that remained provided a bonding surface for the glue on the transmitter cloth and long hair surrounding the positioned disc was then glued over the dorsal surface of the cloth and transmitter. Given the small size of the animal and the saline nature of its environment, battery size (hence longevity and range) had to be traded against weight of the waterproofing agent protecting the unit. Total weights of transmitter packages were approximately 1.8g (collar) and 1.3g (glue-on). As recapture of individual rats was unreliable, collars were abandoned early in the study in favour of glue-on units that could be removed more easily by the rodents. A drawback associated with glue-on units was the ability of rats to twist around and bite the transmitter package. Any intrusion of saltwater into the unit resulted in electrolysis that rendered it inoperable. Glue-on units usually only lasted on an individual for two nights. A 2000 channel 'Regal 2000' (Titley) portable receiver operating on the 150.000-151.999MHz band, and a 2 element hand-held H-frame antenna were used to locate animals.

**HOME RANGE DETERMINATION.** Home range estimates were determined between May 1992 and March 1993 for four adult females, four adult males and one sub-adult male (Table 3). Because visits to the area were irregular and

transmitter life was often unpredictable, animals were tracked soon after capture and thereafter for one or two nights. Length of tracking period was always dependent on the time of capture measured against height and time of the night high tide. As animals usually stayed in their nest until the tide receded, up to four hours of telemetry might be lost in a night to a high tide. All *X. myoides* studied on North Stradbroke were nocturnal. Tracking was continuous and direct observation was used to maximise return of ecological information. Places visited on a rat's traversed route were marked with flagging tape complete with time of recording and subsequently surveyed during the day.

The pattern of habitat use by *X. myoides* was not uniform throughout its entire home range and a percentage usage pattern defined by the 95th and 65th percent probability isopleth proved a most desirable method for estimating home ranges and core areas. Swihart & Slade (1985) have commented that direct observation through continuous tracking may lead to an underestimation of home range size through loss of independence of fixes. To test this, ten-minute fixes were extracted from examination of each of the nine routes plotted through time. Home range estimates arrived at through this method greatly underestimated observed patterns of usage and failed to demonstrate a picture of overlap. Fixes taken for each animal followed are outlined in Table 3. Estimates of home range area were generated using the harmonic mean distance minimum (HM, see Dixon & Chapman, 1980) and the minimum convex polygon (MCP: Mohr, 1974). The utility and appropriateness of the HM for describing home ranges of small, fast-moving mammals was demonstrated by Quin et al. (1992). Estimates were generated with the RANGES 4m computer package.

**SPOTLIGHTING, DIET ASSESSMENT AND NEST ENDOSCOPY.** Radio-tagged animals

	N	Mean	OR	SD	CV
Head-Body Length					
adult (>35g)	42M	102.4	86.4-123.3	8.32	8.12
	26F	98.3	83.1-119.8	8.84	8.99
sub-adult (28-35g)	7M	91.6	83.4-99.0	5.17	5.64
	23F	88.6	76.0-103.5	6.03	6.80
juvenile (<28g)	5M	81.1	70.2-94.1	7.75	9.56
	7F	81.9	62.3-94.8	10.27	12.54
Tail-Vent Length					
adult	43M	81.8	69.3-90.0	5.32	6.50
	26F	80.0	74.4-87.5	3.90	4.87
sub-adult	7M	76.0	67.8-91.0	7.56	9.94
	23F	73.8	67.7-84.2	4.16	5.64
juvenile	5M	63.8	59.0-70.8	4.48	7.02
	7F	67.7	59.7-74.1	4.30	6.35
Hind Foot Length (su)					
adult	43M	23.2	21.6-24.6	0.75	3.23
	26F	22.1	21.0-24.1	0.70	3.17
sub-adult	7M	22.9	22.0-24.0	0.68	2.97
	23F	21.7	20.9-22.8	0.54	2.49
juvenile	5M	20.6	19.9-22.0	0.78	3.79
	7F	21.0	19.7-21.7	0.74	3.52
Ear (from notch)					
adult	42M	12.5	10.5-14.0	0.72	5.76
	25F	12.5	10.7-14.4	0.79	6.32
sub-adult	7M	11.8	11.2-12.3	0.37	3.13
	23F	12.1	10.1-13.8	0.87	7.19
juvenile	5M	11.7	10.4-13.1	1.02	8.72
	6F	11.8	10.0-12.8	0.96	8.13
Anal-Genital Distance					
adult	42M	17.3	10.8-23.2	3.34	19.31
	23F	7.0	4.1-9.7	1.45	20.71
sub-adult	7M	14.1	12.5-17.3	1.52	10.78
	22F	5.8	3.5-7.0	0.79	13.62
juvenile	5M	11.2	8.0-16.2	2.79	24.91
	7F	6.1	5.4-6.4	0.37	6.06
Weight (g)					
adult	42M	46.6	36.0-59.0	6.04	12.96
	26F	42.0	36.0-54.0	5.06	12.04
sub-adult	7M	32.0	28.0-35.0	2.39	7.46
	23F	31.5	28.0-35.0	2.20	6.98
juvenile	5M	21.8	18.0-26.0	3.12	14.31
	7F	24.1	18.0-27.0	3.36	13.94
Spotting					
adult	43M	40	3		
	26F	25	1		
sub-adult	7M	5	2		
	23F	15	8		
juvenile	5M	0	5		
	7F	4	3		

TABLE 2. Measurements, and incidence of dorsal spotting for *Xeromys myoides* from North Stradbroke Is. N=number, OR=observed range, SD=standard deviation, CV=coefficient of variation. Lengths in mm.

were observed with 'Mag-Lite' (Mag Instruments, Ontario, Calif) torches. The expanding beam of these torches greatly facilitated detection of rats moving among mangrove roots. A total of 57 hours was spent observing wild *X. myoides* (Table 3). Rats were more difficult to locate inside densely vegetated communities (e.g., Rainbow Channel), but in areas of low vegetation complexity (e.g., Canalpin Creek, Chiggil Chiggil) the white bellies of running rats were conspicuous. Animals were generally silent and in torchlight the eyes reflected poorly (dull mauve). The diet was assessed by directly observing (with binoculars) radio-tagged rats while they fed, and by the analysis of middens attributed to the rats. Rats were interrupted soon after they began to eat soft prey and the food remnants were pirated for identification. Crustacean prey were identified from skeletal fragments collected after the meal. Faecal pellets were sampled from many animals, but apart from parasites, their contents consisted mostly of minute fragments of unidentifiable crustacean shell and integument.

Non-intrusive observation inside nesting-mound tunnels, nest chambers and of nestling young was facilitated by the use of an endoscope (Olympus GIF type P2) and cold light supply (Olympus CLE-3) powered by a portable Honda 240V generator. Extensive convolution of tunnels in nest mounds made it impossible to reach nest chambers if the endoscope was inserted through a natural entrance. However, it was possible to reach nest chambers using a 15mm-wide hollow coring rod (fibreglass fishing rod) pushed and twisted gently into the roof of the mound. When a lack of resistance in the passage of the rod was detected, the coring rod was extracted, cleaned out, reinserted, and the flexible endoscope tube then introduced and an examination of the area made.

**STUDY SITE AND HABITAT.** At each site surveyed for *X. myoides*, all mangrove species were noted and the vegetation was classified visually according to density and height into one of the community types of Dowling (1986) described below.

North Stradbroke Island, which forms the major part of the eastern boundary of Moreton Bay, lies 40km east of Brisbane. The island is triangular in shape, 36km long from north to

south and about 285 km<sup>2</sup> in area (Fig. 2). Physiography, geology, soils, climate, hydrology and plant communities of this humid subtropical island are broadly outlined in Stevens & Monroe (1975), Clifford & Specht (1979), Covacevich & Durbidge (1981) and Coleman et al. (1984). North Stradbroke Island's western mangrove communities facing the shelter of Moreton Bay are characterised by three ubiquitous and dominant plant species (*Avicennia marina*, *Rhizophora stylosa* and *Bruguiera gymnorhiza*) of wide ecological amplitude, i.e., tolerant of a wide range of salinity and temperature regimes (Bunt et al., 1982). The drainage basin supporting the mangrove communities is in a relatively low-rainfall range (Dunwich annual precipitation 1602 mm) but with an intermediate to low run-off coefficient (ratio of run-off to rainfall, 0.2-0.5) which, given the island's extensive swamps, overflow basins, dense vegetation and sandy substrate, allows considerable retention of water with more regulated and sustained release to the drainage systems (Hutchings & Saenger, 1987). However, in backing onto *Melaleuca quinquenervia* swamps and other poorly drained areas, as commonly is the case, the full development of many mangrove zones is impeded in comparison to those zones abutting better drained and drier areas (Dowling, 1979).

The mangrove communities most commonly associated with this study (Table 1) comprised *Avicennia marina* var. *australasica*, *Rhizophora stylosa* and *Bruguiera gymnorhiza*. Two other species, *Aegiceras corniculatum* and *Ceriops tagal* var. *australis* were more commonly represented toward the southern end of the island. Species descriptions and community compositions for this group in Moreton Bay can be found in Dowling (1986), from which only broad characteristics relevant to this study are summarised below.

*Avicennia marina* var. *australasica*, the most common and widespread species found in Moreton Bay, occurs in any part of the intertidal zone, either as a pure stand or mixed with other species, but usually as an emergent. It is also the most variable species in Moreton Bay, being represented as large, well-developed trees from 10-12 m (or more) tall, or as small spreading shrubs only 0.5 m tall when fully developed. Its growth is tallest and most vigorous when this species stands at the extreme seaward edge in well-drained soils that are inundated by all high tides. At the upper tidal limits its growth is less vigorous and it usually occurs as a small shrub. In areas of

poor drainage, but frequent tidal inundation, *A. marina* forms a low spindly tree. Where freshwater seepage occurs this species tends to form stunted, round, leafy bushes. Death of *Avicennia marina* occurs with waterlogging, ponding of water and siltation leading to the covering of pneumatophores. The structural forms of *Avicennia marina* encountered during this study ranged from Low open-shrubland, Low shrubland and Open-heath (mapping unit 2), Tall open-shrubland and Tall shrubland (mapping unit 3), Low open-woodland, Low woodland and Woodland (mapping unit 5) and Low open-forest and Open-forest (mapping unit 7) (Fig. 7; see Dowling, 1979, 1986 for definitions and descriptions).

Throughout Moreton Bay, *Rhizophora stylosa* occurs either as solitary trees, in clumps of three to five, or in pure stands of densely-packed trees. It may also occur in association with other mangrove species as a large, single-stemmed shrub or small tree toward the lower tidal limits or occasionally in a very narrow zone behind the seaward fringe of *A. marina*. Freshwater from *Melaleuca* swamps is thought to stunt the development of this species (Dowling, 1986). In the study area *R. stylosa* grew in both isolated clumps and in thick belts. Trees growing in clumps were represented by individuals of different heights (1-4 m) and age. Belts of this species were found behind the seaward fringe of *Avicennia marina* and extended to the landward edge. Here the trunks were more erect and unbranched, the prop and stilt roots tangled to 1 m above the ground and the branches did not spread laterally. Structural forms of *R. stylosa* encountered during this study consisted of Tall shrubland, Open-scrub and Closed-scrub (Fig. 8; mapping unit 18, Dowling, 1986).

*Bruguiera gymnorhiza* occurs in Moreton Bay as scattered plants or small clumps of 10-15 trees on the most landward fringes. It is found on hard consolidated muds or peaty clays and is most common in areas of freshwater seepage from the supralittoral zone. In the study area it did not occur in communities, but as solitary trees up to 4 m or small clumps (two to five trees).

*Aegiceras corniculatum* (2 m tall) occurred adjacent to the reed zone on the landward side of the Canalpin Creek and Stockyard sites. This species grows on firm muds which have a shallow layer of soft mud on top. It grows on poorly-drained soils that are shallowly inundated by most high tides. Structural forms encountered included Low open-shrubland and Open-heath (mapping unit 9).





FIG. 7. *Avicennia marina* low open-woodland, Rainbow Channel (Bruce Cowell).



FIG. 8. *Rhizophora stylosa* open-scrub, Rainbow Channel (Bruce Cowell).

*Ceriops tagal* var. *australis* occurred only at the upper tidal limit of the Stockyard site. Normally, *Ceriops* communities are inundated only by a few tides each month, and they occur on firm, well-drained clays, clayey muds or sandy clays. The structural forms encountered included Tall open-shrubland, Tall shrubland, Open-scrub and Closed-scrub (mapping unit 15).

The floor of the mangrove community provided an array of microhabitats including tidal pools, channels, crab holes, pneumatophores, crevices in bark and around roots, hollows in standing and fallen timber, suspended drifts of twigs and leaves, driftwood, detritus and tide-washed garbage. The complexity of microhabitats varied according to the structure of the mangrove community. Highest structural floor diversity occurred in the species-rich communities at Rainbow Channel (Fig. 8) followed by those at Stockyard. Lowest structural floor diversity occurred in the *Avicennia* woodlands of Canalpin Ck and Chiggil Chiggil.

On the landward side, mangroves were abutted by either a discrete zone of sedgeland, *Melaleuca quinquenervia* swamp/*Eucalyptus robusta* forest alliance, or heathland (Fig. 9). The sedgeland band (1.2m high) in which salinity is reduced by drainage from the mainland, comprised almost exclusively *Juncus kraussii*, *Baumea juncea*, *B. rubiginosa* and *Fimbristylis ferruginea*. In many places this zone was up to 30m wide and was sharply delineated from both the upper reaches of the mangrove woodland tract and the lowest extent of the wallum (dominated by *Melaleuca quinquenervia*, *Eucalyptus intermedia*, *E. robusta*, *Leptospermum livensidei*, *Gahnia sieberiana* and *Caustis blakei*).

Supralittoral banks, formed by the combined effects of spring tides, wind setup and storm



FIG. 9. Aerial view of Rainbow Channel study site showing zonation from marine meadow (bottom) through mangrove community and sedge zone to freshwater swamp/wallum woodland (top) (Bruce Cowell).

surge, occurred at the sedgeland/wallum or mangrove/freshwater marsh ecotones. The Canalpin supralittoral bank, at 95cm high, was the tallest bank encountered. In some areas (e.g., Deanbilla) it was poorly defined. In most areas where this bank abutted wallum, the groundsel *Baccharis halimifolia* was a dominant species along the bank. After periods of rain, freshwater percolated through the supralittoral banks and the integrity of the bank depended on its consolidation by the roots of salt-tolerant species such as *M. quin-*

TABLE 3. Home Range estimates, linear distances covered and allocation of time in *X. myoides*. HM 95% = 95% isopleth of the Harmonic Mean Measure, MCP=Minimum Convex Polygon, Dist(m)=linear distance covered during observation time (Obs. time).

Animal	Date	#Fixes	Home Range (ha)			Dist(m)	Obs. time	Foraging	Grooming
			HM 95%	Core 60-65%	MCP				
AF4	2.5.92	35	0.41	0.13-0.18	0.45	599	4hr 54min	89.3	14.7
AF21	28.1.93	25	0.46	0.10-0.16	0.30	307	1hr 36min	100	0.0
AF31	20.8.92	67	0.30	0.23-0.33	0.82	833	5hr 21min	68.2	31.8
AF62	10.12.92	59	0.30	0.22-0.32	0.54	1053	3hr 14min	92.8	7.2
AM16	27.7.92	57	0.93	0.10-0.13	0.86	895	5hr 00min	67.3	32.7
AM33	22.8.92	120	0.65	0.19-0.22	0.76	2170	9hr 32min	94.5	5.8
AM68	3.12.92	126	0.77	0.24-0.29	0.74	1227	2hr 48min	95.8	4.2
AM89	20.3.93	105	7.35	0.47-1.06	3.42	2891	9hr 11min	86.9	13.1
SAM34	11.9.92	38	0.38	0.12-0.17	0.50	514	2hr 34min	87.7	12.3

*quenervia* and *Casuarina glauca*. Where these species were absent (e.g., Canalpin), the supralittoral bank experienced dramatic scouring and profile changes.

## RESULTS

**DISTRIBUTION AND TRAPPABILITY.** *Xeromys myoides* was recorded from all island mangrove communities surveyed between Chiggil Chiggil and Stockyard (see Table 1).

The species was apparently not trap-shy. A total of 111 *X. myoides* individuals were trapped and 24 individuals were retrapped (Table 5). Trapping success for new captures was higher in mangrove transects compared to 'barricade' trapping where up to eight traps were set in a ring around a nesting mound in sedgeland (total traps set in mangroves = 606, trapping success for first captures = 11.7%; total traps set around sedgeland nest = 710, success for first captures = 3.9%). Overall success (first captures and recaptures) from mangrove vs. nest settings was slightly higher in mangroves (mangrove trap success 11.4%, nest success 8.4%). The total number of sub-adult males trapped (seven) was low. If traps were left open through the day high tide, bait was usually eaten by toadfish (*Tetractenos hamiltoni*, *Marilyna pleurostricta*) or traps were upturned by Mud Crabs (*Scylla serrata*).

Capture of taxa other than *X. myoides* was rare. Five *Melomys burtoni* were caught (Capembah Creek, 1 & 4 May 1992 at the mangrove/dry woodland ecotone, two individuals; and Deanbilla, 25 September 1992 in mangroves; three individuals); *M. cervinipes* was trapped at Deanbilla, 26 November 1992 in mangroves (1 individual); and two *Rattus lutreolus* were caught

at nest-site G of *X. myoides* at Rainbow Channel, 1 May 1992 and 22 August 1992 at the sedgeland/dry woodland ecotone. Cane Toads (*Bufo marinus*) were frequently seen or caught in sedgeland traps in the Rainbow Channel site and in mangroves of the Canalpin Creek site. One Lewin's Rail *Rallus pectoralis* was trapped overnight in sedges at nest-site B, Rainbow Channel. Surprisingly, no *Hydromys chrysogaster* were seen or trapped during the study, although the dismembered remains of a large Mud Crab (*Scylla serrata*) were noted at Myora Springs. The presence of the Water Rat was suspected at the Rainbow Channel site where numerous traps were found tripped, their baits removed and eaten close by.

During the study only one *Rattus rattus* was observed (running along the prop roots of *R. stylosa* trees), but numerous middens and food caches attributed to that species were recorded in trees. Measurements of *Xeromys myoides* from North Stradbroke Island appear in Table 2.

**NESTING.** *Xeromys myoides* nested in a wide variety of sites, and nest forms varied considerably, ranging from large termitarium-like mounds up to 60cm high built in the marine sedgeland (Fig. 10) to inconspicuous tunnels excavated in the supralittoral bank at the marine-sedgeland/freshwater-wallum ecotone. Six large mounds were recorded from within the Rainbow Channel site and one from Stockyard. Adjacent nest mounds were separated by distances of between 80 and 410m. Mounds were constructed of a mixture of excavated peat, sedge straw, mud and sand. They were from 20cm to 60cm high with basal circumferences from 1.6m to 4.8m. From one to three entrance holes were found at each

TABLE 4. Residency in nest mounds presumed to be used by more than one animal. Individuals trapped at nest. \* Individuals re-trapped in mangroves directly in front of nest. # Transmitter day-fix.

Nest	Animal No.	Age	Sex	Capture Date	Recapture Date(s)
H	1	A	M	26.2.92	-
	27	A	M	6.8.92	21.8.92*
	26	A	F	6.8.92	-
	28	SA	F	6.8.92	-
	8	SA	F	18.6.92	-
	13	J	M	3.5.92	-
A	16#	A	M	16.7.92	18.19.27.28.7; 10.12.92*
	3	A	F	1.5.92	2.5;17.6.92
	34#	SA	M	21.8.92	22.8;10.9.92
	7	SA	M	17.6.92	18.7.92
	17	SA	F	17.7.92	27.1.93*
	12	SA	F	2.5.92	3.5;16.7;17.6.92
	25	SA	F	28.7.92	-
	11	J	F	2.5.92	3.5;17.6.92
B	2	A	F	20.11.91	-
	4#	A	F	2.5.92	17.6.92
	18	SA	M	17.7.92	-
	19	SA	F	17.7.92	27.7;22.8.92
D	24	A	M	27.7.92	-
	20	A	F	17.7.92	18.7;19.7.92

mound, but others may have been hidden under the labyrinth of exposed tree roots into which mounds were often incorporated. The number of entrance holes at any one nest varied throughout the year, with disused holes quickly filling in. Regularly used holes were oval in shape (approximately 60mm by 40mm) and positioned anywhere from the top to the bottom of mounds; holes were from 30cm to 2m apart. Although lower holes were flooded at high tide, the mounds themselves were never seen to have been entirely inundated (Fig 11).

Evidence of external mound 'workings' consisted of fresh roof 'plasterings' in which a thin black paste of mud mixed with peat, dried leaves, sedge stems, or crab shells had been daubed over the top of the mound and worked between sedges (usually *Juncus kraussii*). Areas 'plastered' in this way measured as much as 0.12m<sup>2</sup> and in many cases a semi-tubular path of fresh plastering covered a track from the nest entrance hole up or around to the nest top. The absence of fresh plastering did not indicate that the nest was unoccupied, as plastering was an infrequent event. Nest-site G was first noticed on 15 Nov 1991 as

TABLE 5. Recaptures of *Xeromys myoides* (by sex, age and individual number) at Rainbow Channel.

Age	Indiv. No.	Date	Weight (g)	Age	Indiv. No.	Date	Weight (g)
Female				SA	19	17.7.92	28
A	3	1.5.92	43	J	11	27.7.92	28
		2.5.92	43			22.8.92	28
		18.6.92	46			2.5.92	27
A	4	2.5.92	54			17.6.92	26
		18.6.92	41	Male			
A	20	17.7.92	36	A	16	16.7.92	43
		17.7.92	36			17.7.92	43
		18.7.92	36			18.7.92	43
		19.7.92	36			19.7.92	44
A	21	17.7.92	40			27.7.92	44
		17.7.92	40			28.7.92	44
		21.8.92	40				
A	26	6.8.92	37	A	27	6.8.92	38
		6.8.92	37			21.8.92	41
A	31	20.8.92	39	A	33	20.8.92	48
		22.8.92	39			22.8.92	48
A	56	19.9.92	40	A	36	21.8.92	43
		20.9.92	40			22.8.92	43
A	59	21.9.92	47	A	38	21.8.92	41
		21.10.92	42			21.8.92	41
A	66	22.8.92	37	A	82	27.11.92	50
		22.8.92	37			28.11.92	50
SA	12	2.5.92	33	A	93	24.5.93	53
		17.6.92	32			25.5.93	53
		16.7.92	32				
		17.7.92	32				
		21.8.92	37				
SA	17	22.8.92	37	SA	7	17.6.92	33
						18.7.92	38
SA	17	17.7.92	31	SA	18	17.7.92	35
		18.7.92	31			17.7.92	35
		19.7.92	31				
		27.7.92	23				
				SA	34	21.8.92	32
						22.8.92	32
				J	9	10.9.92	34
						2.5.92	26
						17.6.92	33

a reed-covered hole in the supralittoral bank accompanied by traces of plaster in the reed bases. By March 1993, plastering had built the mound up by 6cm and the entrance hole had been moved to the top.

Three mounds were built on slightly elevated islands supporting small patches of stunted *Melaleuca quinquenervia* and *Casuarina glauca*. One of these nests incorporated the stem of a living *Vitex trifolia* var. *bicolor* (Figs 10, 11).

Tunnels in the supralittoral bank (shaped and maintained by spring tides) were inconspicuous and generally only found by radio-tracking individuals trapped and released in the mangroves.



FIG. 10. Large nesting mound (B) built in the marine sedgeland at Rainbow Channel.



FIG. 11. Nesting mound (B) moated by high tide, Rainbow Channel.



FIG. 12. *Xeromys myoides* despatching a Red-fingered Crab *Parasesarma erythrodactyla*, the most commonly eaten crustacean. (Bruce Cowell).

Four were recorded in the Rainbow Channel site and confirmed by radiotelemetry and two were recorded and confirmed from Canalpin Ck. The face of the bank, and hence the location of entrance holes, changed dramatically at Canalpin Ck with erosion of the bank caused by spring tides and freshwater runoff.

Several indications from radio-tagged individuals suggested that *Xeromys myoides* built, or at least used, extensive and complex burrow networks inside and above the supralittoral bank. One male (AM33) covered approximately 20m underground after returning to its nest when a high tide restricted foraging in the mangrove zone. One female was recorded using a system of burrows through *Galinia*-dominated freshwater swamp 10m behind the supralittoral bank at Canalpin Ck. The peat substrate of both these areas may facilitate a significant subterranean facet of life history as yet unsuspected in this species. Alternatively, *Xeromys* may have been using tunnels constructed by *Rattus lutreolus*, an extremely common species in these areas.

Although large termitarium-like nesting mounds are known to be occupied and maintained by groups of rats, the rodents' proclivity for unpretentious nesting in supralittoral banks suggests that some large nesting mounds may represent physical, historic evidence of the past position of the supralittoral shoreline. The rat's demonstrated ability to consolidate and add to

a mound, as well as the likelihood of a mound overgrowing with sedges and small trees, both increase the chances of a nest-site remaining when the rest of the bank erodes through spring tides and heavy wave action. The maintenance and extension of a nesting mound may represent a response by the occupants to a wet nesting chamber during high tides.

Over the course of the study, mound nests were found to contain animals of all three age categories (adult, sub-adult and juvenile) and of both sexes (Table 4). However, no more than one adult male was recorded concurrently in the same mound (other sexes and age categories were recorded). Adult males were observed visiting neighbouring nests during

the night, so a capture at a nest site did not necessarily imply occupancy. Adult females were noted to avoid entering a co-mounding female's burrow and if released into a 'wrong' tunnel would quickly turn around, exit the burrow and run across the mound to their 'own' tunnel. Endoscopic examination of one nesting mound (A) revealed extensive tunnel systems through the mound, with two nesting chambers within the top 16cm. Each nest was lined with the dried leaves of *Melaleuca quinquenervia*, which also littered areas around the mound. Mounds and bank tunnels provided humid protection not only during the day, but during night high tides when most *X. myoides* returned to their nests (presumably to avoid the water). One instance was noted of a



FIG. 13. Unnamed marine polychaete (30mm long), featuring in the diet of *Xeromys*. (Bruce Cowell).



FIG. 14. Marine pulmonate *Ophicardelus quoyi* showing breaches made by *Xeromys* (Bruce Cowell).

male remaining in a hollow of a mangrove trunk during a night high tide.

**DIET.** The following are food items recorded by direct observation of wild *X. myoides*.

**Crustacea.** The small crab *Parasesarma erythro-dactyla* was the most commonly recorded prey item taken inside the mangrove zone. *Xeromys myoides* ate both adults and minute juveniles (see sizes documented below). The manner of dispatching a crab was as described by Redhead & McKean (1975); crabs were first disarmed of claws, legs were bitten off, and the body turned over and breached from the softer ventral side (Fig. 12). The meat was scoured from the inside of the carapace. In some instances rats were observed to bite adult crabs between the eyes then drop and leave them, but return after a few minutes to consume the catch under suitable cover. Carapaces and basal leg segments were left uneaten, but claws were sometimes hollowed out. *Parasesarma erythro-dactyla* was observed being consumed by four *X. myoides* (AF4, AF31, AM34, AM89) in the months of March, May and August.

*Helice leachi* (one specimen, carapace width 20mm) and *Australoplax tridentata* (one specimen, width 15mm) were recorded in the diet of AM89 at Canalpin Ck on 20 March 1993.

**Marine polyclads.** An undescribed marine polyclad (Fig. 13) was recorded in the diet of adult female (AF4) at Rainbow Channel, 3 May 1992. Two instances of polyclad predation were recorded on the same night. Under studio conditions, another adult female was photographed feeding on the same species. Polyclads were regularly recorded sheltering in rotting driftwood washed to the dry supralittoral zone. As many as

14 were once recorded from inside the honeycombed core of a small log (45cm long x 10cm diameter). There have been no other recorded predators of marine polyclads (L. Cannon pers. comm.).

**Marine pulmonates.** *Ophicardelus quoyi* (Fig. 14) was recorded being eaten by an adult female (AF4) at Rainbow Channel on 11 May 1992 (and were readily eaten by animals held in captivity). These small pulmonates gathered under driftwood in the middle of the sedgeland. Female AF4 was heard cracking *O. quoyi* under

a large plank. On examination, a midden of opened shells was found in a concavity clipped from reeds flattened under the plank. All shells had been breached through the body of the shell, and not through the aperture.

*Salinator solida* (Fig. 15), a small (8mm) periwinkle-like mollusc was recorded from the diet of an adult male (AM89) at Canalpin Ck on 19-20 March 1993, and was present in numbers in a Chiggil Chiggil midden. Entry to the body of the pulmonate appeared to be through the aperture as no retrieved specimens were breached.

*Onchidina australis*, a large (30mm), shell-less slug was eaten by an adult male (AM89) at Canalpin Ck on 20 March 1993. Parts of the gut were left uneaten.

**Marine bivalves.** *Glaucanome* sp. (Fig. 15), a small (11mm) sea-green mussel was eaten by an adult male (AM89) at Canalpin Ck on 20 March 1993. Opened halves of this bivalve were commonly observed across the mangrove floor, but none was recorded in *Xeromys* middens.

The following Crustacea are food items recorded from middens which were attributed to *X. myoides*:

*Parasesarma erythro-dactyla* was the most common component of mangrove middens. One midden inside the base of a hollow *Avicennia* at Chiggil Chiggil contained 14 carapaces of this crab (average width 12mm, range 10-16mm) and four of *Helice leachi* (average width 17mm, range 15-20mm). Largest carapaces of *P. erythro-dactyla* believed to have been consumed by *X. myoides* measured 20mm in width. *Helice leachi* was the most commonly recorded component of supralittoral middens. A sample of carapaces taken from a Chiggil Chiggil reed zone midden





FIG. 15. Prey taken by *Xeromys* on North Stradbroke Island, (anti-clockwise from crab) Red-fingered Crab *Parasesarma erythrodactyla*, Sea-green Mussels *Glaucanome* sp., marine pulmonates *Ophicardelus quoyi* and *Salinator solida*, unnamed marine polyclad (Bruce Cowell).

known to be used by an adult female (AF55) contained 36 carapaces (average width 17mm, range 13-21mm) and three of *Parasesarma erythrodactyla* (average width 13mm, range 11-14mm). *Peragrapsis laevis* (four specimens, average width 17mm, range 13-23mm) was recorded from a hollow *Avicennia marina* ground level spout known to be frequented by an adult female (AF31) at Rainbow Channel. Skeletal remains of the mud lobster *Laomedia healyi* were collected on 20 Aug. 1992 and 16 Sept. 1992 from a hollow *Avicennia marina* ground level spout known to be frequented by an adult female (AF31). **Diet in Captivity.** Captive specimens of *X. myoides* consumed relatively large quantities of food. During the period 20 Feb. 1995 – 4 March 1996 the average weight of raw prawns consumed daily by an adult female (of average weight during that period 38g) was 22g representing an average daily intake of 57.8% body weight (at ambient temperature 24°C). For a period of eight weeks (18 Sept. 1995 – 13 Nov. 1995) this

animal maintained body weight (average weight 38.0g, 35-40g range) on a raw prawn diet with no access to free water.

**FORAGING BEHAVIOUR.** Observed radio-tagged individuals of *Xeromys myoides* spent their foraging hours dashing over the substrate between trees, 'snaking' through pneumatophores and investigating hollows in mangrove trunks. Their nocturnal behaviour was generally frenetic although animals were recorded to rest inside a favoured mangrove hollow for periods of up to three hours. Linear distances covered and times spent foraging are shown in Table 3.

Generally rats left their nests and followed the receding tide out through the sedgeland and into the mangroves where they foraged. In so doing they passed through a 'common' corridor between the nest and the foraging area. In some cases this precipitated meetings (usually brief and violent) with other rats or an inspection of





FIG. 16. Typical resting hollow in an *Avicennia marina* base, Rainbow Channel (Bruce Cowell).

neighbouring nests. Animals scoured their home range during the course of an evening.

Animals visited and revisited favoured haunts such as hollows in *Avicennia* trunks, *Rhizophora* root tangles and hollow fallen logs. Large food items such as adult crabs were taken to favoured hollows (Fig. 16) where the item was consumed under cover. With time, discarded food items formed recognisable middens (Figs 17, 18). All nocturnal resting took place in such hollows. Animals climbed up inside gently sloping trunk hollows to about 1 m, but no arboreal activity was ever recorded. The favoured 'pathways' of *X. myoides* were those that ran closely alongside the low, long prop roots of *Rhizophora stylosa*, under the canopy of twigs and leaves deposited on the tops of prop roots by the fallen tide, or alongside fallen logs. In open areas of *Avicennia* forest animals ran quickly between trunks and logs in order to regain cover.

**HOME RANGE DETERMINATION.** Home range estimates were made for eight animals (four adult females, three adult males, one sub-adult male) from the Rainbow Channel area and 1 adult male from Canalpin Creek. Results of home range analysis and plots of nests appear in

Figures 19, 20, 21 and Table 3. There was a high degree of correlation between HM and MCP estimates. The 95% isopleth of the harmonic mean distance minimum (HM) gave an average home range area of 0.637ha for the seven adults radio-tracked at Rainbow Channel. The minimum convex polygon (MCP) average for the same seven animals was 0.614ha. The results suggested a greater home range area for males than females (male HM average 0.78 ha, MCP 0.77ha vs female HM average 0.59ha, MCP 0.53ha), but this may have been influenced by the smaller number of fixes available for females. These results should be taken as preliminary and minimal as some plots indicate that the curves had not quite asymptoted (see Quin, et al., 1992; Goldingay, 1992). The home range of the Rainbow Channel sub-adult male (SAM34) was smaller than all other males and less than the female average. The adult male (AM89) from Canalpin Creek had a home range estimated at between 7.35ha (HM 95%) and 3.42ha (MCP). Given the physiographic barriers associated with the Canalpin Creek site (salt water, dry forest and a very narrow band of mangroves, Fig. 21), the MCP estimate represents the most acceptable estimate of home range size. Core areas (averaged from the



FIG. 17. Favoured feeding hollow, in an *Avicennia marina* base, Chiggil Chiggil.



FIG. 18. *Xeromys myoides* midden from Rainbow Channel showing mainly crab shell fragments.

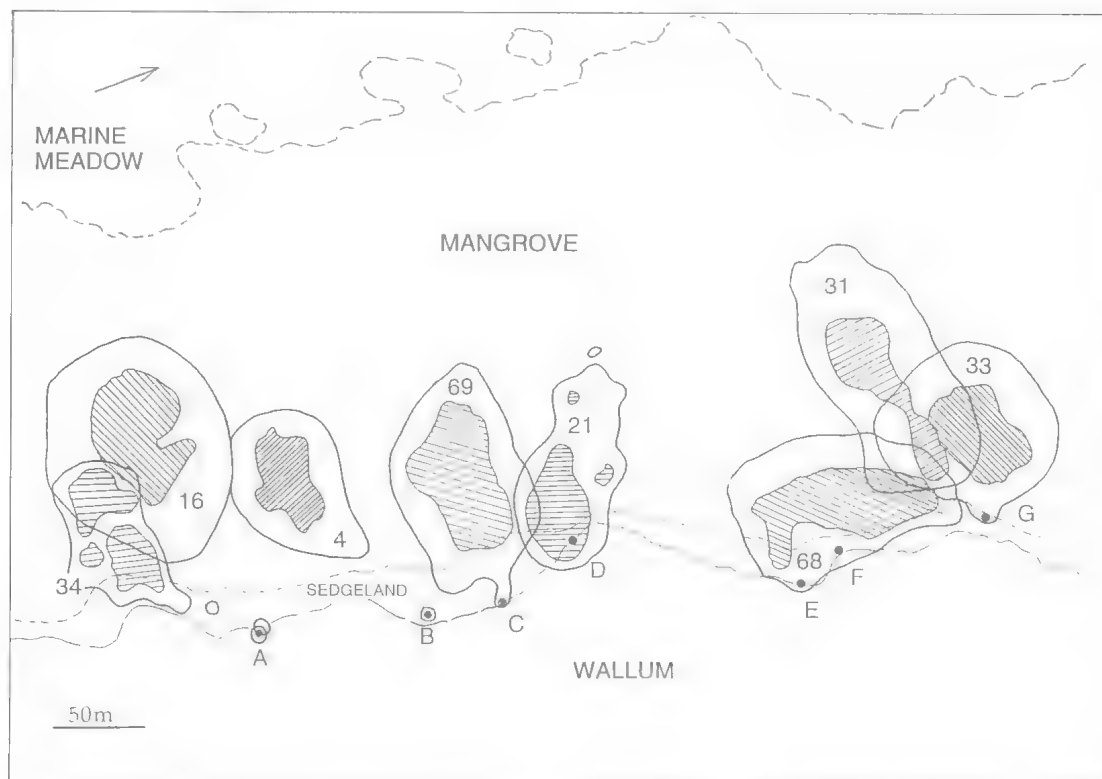


FIG. 19. Home range estimates of eight *Xeromys myoides* individuals from Rainbow Channel (Site 2). For home ranges, solid black lines show 95% isopleths of Harmonic Mean measures, hatched areas represent core areas (65% isopleths). Sub-adult male 34 is from nest A, as is adult male 16, adult female 4 is from nest B, adult female 69 from nest C, adult female 21 from nest D, adult male 68 from nest E, adult female 31 from nest F and adult male 33 from nest G. All nests except B are at the supralittoral ecotone between marine sedgeland and wallum woodland. The arrow points north.

HM 60-65% isopleths) for Rainbow Channel adults averaged around 0.20ha, with adult male core area being estimated at around 0.19ha and adult females at approx. 0.20ha. The Canalpin Creek male had a core area estimated at around 0.76ha. Core areas of the eight Rainbow Channel animals did not overlap, but animals moved in and out of their neighbouring territorial peripheries.

**REPRODUCTION.** Scrotal males were recorded in the population in all months except January, February and April (few traps were set during February, none in April, and one young adult male was trapped in January). Females, presumed to be pregnant by their swollen appearance and increased weights, were recorded in the months of January, May, August, September and October. Females with enlarged nipples were recorded from July through to December. Juveniles were

recorded in the months of May, July, August and November. Little is known of litter size and nothing of the rate of growth of young *X. myoides* on North Stradbroke Island. Endoscopic examination of a nesting chamber in nest site 2 on the night of 26 October 1993 revealed a litter of four dark-skinned but hairless young. On detection of the tip of the endoscope the adult removed each pup separately to another location in the nesting mound.

In the absence of more information it would appear that *X. myoides* is capable of breeding throughout the year.

**PARASITES.** Nematodes were retrieved from the faeces of one adult female *X. myoides* (AF2) and from the stomachs of three subadults (QM JM9478, JM9479, JM9728) and one adult male (QM JM9480). These were assigned to the genus *Tikusnema* Hasegawa, Shiraishi & Rumpus 1992

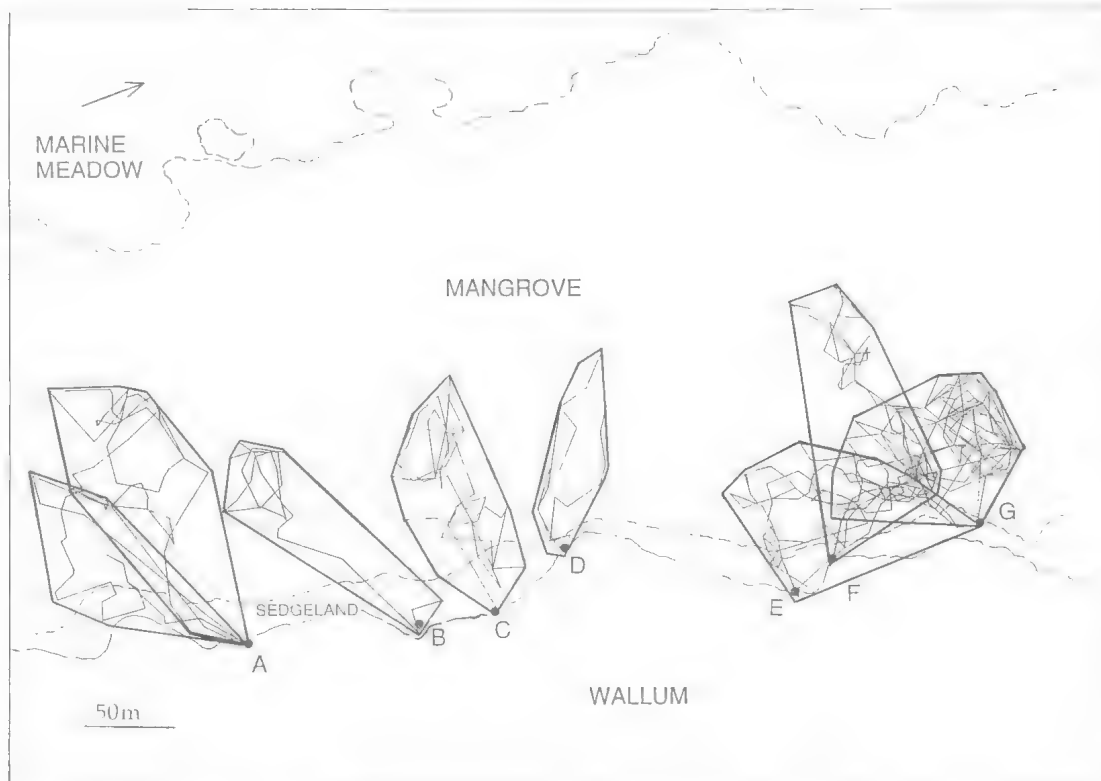


FIG. 20. Home range estimates (Minimum Convex Polygons) and actual trackways recorded for the eight *Xeromys myoides* individuals of Fig. 19, from Rainbow Channel (Site 2). The arrow points north.

as *T. vandycki* Smales, 1995. The implications of the presence of acuariid nematodes, normally found in birds, in *X. myoides* and other small mammalian hosts is discussed by Smales (1995).

Mites, *Mesolaelaps australiensis* (Hirst, 1926), were retrieved from the body and ears of AF3, AF17, AM41 and AM15. This species has been recorded from a wide range of mammals, birds and reptiles in Australia and the South West Pacific (R. Domrow pers. comm.)

Ticks *Ixodes tasmani* were removed from the body of AM41 and from between the toes of the hind foot of AM7.

**PREDATORS AND COMPETITORS.** Carpet Pythons *Python spilotes* were recorded in sedgeland (Nov 1992) and inside mangrove forest (Nov 1992). A 2m specimen draped across *Rhizophora* prop roots approximately 10cm from the floor of the forest at low tide was probably hunting rats. Two Rough-scaled Snakes *Tropidechis carinatus* were recorded in the sedgelands at low tide (25 Feb. 1992, 10 Nov. 1992); one was investigating nest site 2 but was not observed entering any

burrows. Tawny Frogmouths *Podargus strigoides* commonly occurred in woodland adjacent to the mangrove zone but no owls were observed during the study. One frogmouth was observed at Canalpin Creek watching over mangrove flats. A three-syllable *Ninox*-like call was recorded in the Myora mangroves on 26 Oct. 1993 but the identity of the caller was not determined. Dissection of Cane Toads *Bufo marinus*, found feeding in the mangroves of Canalpin Ck revealed a diet consisting largely of crabs, marine pulmonates and amphipods. The crabs were of a similar size to those eaten by *X. myoides*.

It is possible that *Xeromys* may represent a potential prey item for *Hydromys*. Woollard et al. (1978) recorded young *Hydromys* in the diet of adults of that species (particularly males). If this behaviour occurs also in *Xeromys* it may provide one possible explanation (along with early expulsion or killing without ingestion) for the low record of sub-adult (dispersing) males captured during the survey (seven sub-adult males: 23 sub-adult females).

## DISCUSSION

*Xeromys myoides* on North Stradbroke Island is a small, spotted, specialised, non-aquatic, non-arboreal, nocturnal muroid rodent whose life history revolves around the island's western mangrove and adjacent sedgeland communities. The species appears to be carnivorous.

**DIET.** Truly carnivorous species of rodents which ingest more than 50%-80% animal food are very rare (Dieterlen & Statzner, 1981). African examples include the dendromurine rodents *Deomys furrugineus* and *Leimacomys buttneri* (Dieterlen, 1976); murine rodents of the genus *Lophuromys*, *Zelotomys* (Dieterlen, 1976) and *Colomys goslingi* (Dieterlen & Statzner, 1981). Neotropical examples include hesperomyine cricetids such as *Ichthyomys*, *Anatomys*, *Daptomys*, *Neustictomys*, *Rheomys* (Starrett & Fisler, 1970; Voss, 1988) and *Nectomys squamipes* (Ernest & Mares, 1986). Examples from Australia and New Guinea include the hydromyines *Hydromys* (Woollard et al., 1978; Menzies & Dennis, 1979), *Crossomys moncktoni*, *Parahydromys asper* (Menzies & Dennis, 1979), *Leptomys elegans* (Dwyer, 1984), *Mayermys ellermani*, *Neohydromys fuscus*, *Pseudohydromys murina* and *P. occidentalis* (Jackson & Woolley, 1993) and probably also the genera *Paraleptomys* and *Microhydromys* (Menzies & Dennis, 1979; Flannery, 1990).

Carnivore digestive systems are noted for their simple stomachs, short small intestines, short large intestines and short or absent caeca (Hume, 1982). Barry (1977) commented that for most rodents, relative gut lengths are inaccurate indicators of relative absorptive surface area, given that a large proportion of the total absorptive surface of the hindgut may be found in the small intestine although this might account for a relatively small proportion of the total length. However, Barry also noted that for more carnivorous forms, relative lengths more accurately reflect relative absorptive surface areas because the caecum and colon are greatly reduced in relation to the small intestine. Gut morphology suggests that the diet of *Xeromys myoides* should not be totally carnivorous. Relative alimentary canal dimensions for five New Guinean hydromyines are presented by Jackson & Woolley (1993). The relative length of the small intestine of *Xeromys myoides* (85% of the total gut) is slightly shorter than that recorded for the four New Guinean hydromyines *Mayermys ellermani*, *Neohydromys fuscus*, *Pseudohydromys murinus*

and *P. occidentalis* (Jackson & Woolley, 1993), while the relative length of the large intestine (14%) is longer. However, relative caecum length in *X. myoides* (2%) is shorter than in *Mayermys ellermani*, *Neohydromys fuscus* and *Pseudohydromys occidentalis* and approaches the relatively short caecum length found in *P. murinus* (1%). Jackson & Woolley (1993) suggested that, on the basis of gut morphology and dietary analysis, *Pseudohydromys murinus* should not be considered an obligate carnivore. However, they noted that the plant material present in the guts of 22 of 24 sampled specimens could have been contained in the guts of their insect prey.

Relative lengths of the large intestine and caecum in *Xeromys myoides* closely approximate those of *Hydromys chrysogaster* (pers. obs.) which, although recorded eating a wide variety of vertebrate and invertebrate prey (Brazenor, 1936; Troughton, 1941; Barrett, 1955; McNally, 1960; Fleay, 1964; Woollard et al., 1978; Harris, 1978) has rarely been reported consuming vegetation. Brazenor (1936: 66) noted them to eat 'coarse grass or rushes' and Barrett (1955: 119) commented that they were 'partly vegetarian'. Woollard et al. (1978) concluded that plants were consumed as trace items but increased in importance in winter when resources were low. Harris (1978) recorded crustaceans as major prey items of *Hydromys chrysogaster* at three sites in south-eastern Queensland but did not observe animals feeding on vegetation, nor detect vegetation in scats. At two of these sites mammalian prey accounted for up to 9% of prey and 5% of the volume of scats.

Plant foods have, to date, not featured prominently in the diet of *Xeromys myoides*. The components of scats (from five individuals) and entire gut contents (three individuals) have reflected observed feeding preferences (recorded from 9 wild individuals) and included gross items such as mollusc viscera, shell and operculae, crustacean shell and gills, sand and hair (*X. myoides*). Microscopic examination of gut contents has revealed plant material in the form of xylum elements, parenchyma and fibre, probably from mangrove propagules ingested by (probably) crustacean prey (J. Bertram pers. comm.).

**HOME RANGE.** Individuals of *Xeromys* tracked throughout the year in this study at Rainbow Channel had home ranges (95% isopleths) which abutted or overlapped outlying areas of those of their neighbours (Figs 19, 20). However core

areas (65% isopleths) did not overlap. Predictably, adult males had larger home ranges (average MCP 0.77ha) than females (0.53ha) and it was assumed that this reflected an investment of female defence and male repulsion that took the territorial limits beyond the male's dietary requirements. Females had smaller home ranges which, presumably, provided them with quick access to resources as close to their nests (and young) as possible. *Xeromys myoides* stands to gain much from the microhabitat specialisation of the mangrove crab population. At low tide the rats can exploit common species such as *Parasesarma erythroactyla* out toward the seaward limit of the mangroves. During high tides, when access is blocked to the mangrove's most productive zones, those crabs which extend into the high intertidal or terrestrial zones (e.g., *Helice leachi*) can be exploited. Given that large body size does not increase an animals capacity to acquire food, a small size of around 40g (as is the case of *X. myoides*) could be interpreted as the evolutionary optimum for harvesting the commonest of mangrove crabs without resorting to a semiaquatic life style such as that seen in the much larger *Hydromys chrysogaster* (Water Rat).

*X. myoides* appeared to respond more quickly to scent than any other stimulus offered by its prey, and it was suspected that given the daily flushing of home ranges, scent laid down inside erect hollow trunks of living trees might represent a cost effective method of home range familiarisation and territorial defence.

Schoener (1969) predicted that declines of prey abundance might be offset by expansions in either prey types or home ranges. In *Hydromys*, home range size has been shown to be smaller in areas of high substrate complexity, notably a high incidence throughout the home range of aquatic vegetation, stumps, sunken logs, eroded embankments and exposed roots (Harris, 1978). The same appears to be true for *Xeromys* on North Stradbroke Is. At Rainbow Channel the mangrove community is wide (200m from the marine meadow to the sedgeland) and diverse, with dense forests of *Rhizophora stylosa* and *Avicennia marina*. The substrate is complex with abundant trunk and root hollows, labyrinths of prop roots, flotsam rafts of twigs, propagules, leaves and eel-grass suspended on prop roots, a profusion of fallen logs and timber flotsam, and an abundance of tidal pools. Average home range size for adult males (N=3) from Rainbow Channel was 0.78ha (HM), 0.75ha (MCP). At Canalpin

Ck (Site 5), an area of *Avicennia* parkland, the mangrove zone was mostly narrow (maximum 20m), with widely spaced (average 5.2m) mature trees and very low substrate complexity. The home range of the only adult male (A89) tracked at Canalpin Ck was larger at 7.35ha (HM), 3.42ha (MCP). From its nest in the supralittoral bank, this male emerged to follow the line of the supralittoral bank for 300m to an area of greater microhabitat diversity and broader mangrove width where it foraged until returning to its nest at dawn (Fig. 21).

Structural diversity of the mangrove community and substrate microhabitat complexity probably determine centres of reproduction and dispersal on the island. In this respect, the communities of the Rainbow Channel and Stockyard represent the most important conservation zones for the species on, and close to, North Stradbroke.

Harris (1978) recorded lower weights in *Hydromys* from freshwater compared to estuarine habitats, and suggested that this reflected a difference in the quality of the two habitats. Although False Water-rats have been recorded in both habitat types throughout its east Australian range, no significant foraging took place inside the freshwater marshes and paperbark swamps immediately accessible to all radio-tagged individuals from Rainbow Channel or Canalpin Creek. Similarly, the outer (marine meadow) extremity of the mangrove zone, dominated by more widely separated, more mature *Avicennia*, was avoided. This study suggested that at these two localities, the most productive zone lay somewhere between *Xeromys* nests at the supralittoral bank and the first 100 metres into the mangroves.

**AQUATIC ADAPTATION.** There has been much speculation on the level of aquatic adaptation achieved in *Xeromys*. Thomas (1889) treated it as a terrestrial rat, Troughton (1954: 273) regarded it as 'an aquatic-feeding land rat', Redhead & McKean (1975: 352) contended that it was 'clearly ... aquatic', and Magnusson et al. (1976: 157) concluded that '*X. myoides* is basically a terrestrial rat that feeds on hard-shelled aquatic fauna'.

Results of this study indicate that *X. myoides* (on subtropical North Stradbroke Island at least) cannot be described as aquatic. Indeed, on a broad scale, the species scarcely qualifies as semiaquatic. Voss (1988), comparing a range of small (14-202g) semiaquatic-carnivorous lipotyphlans and Old World muroid rodents against closely

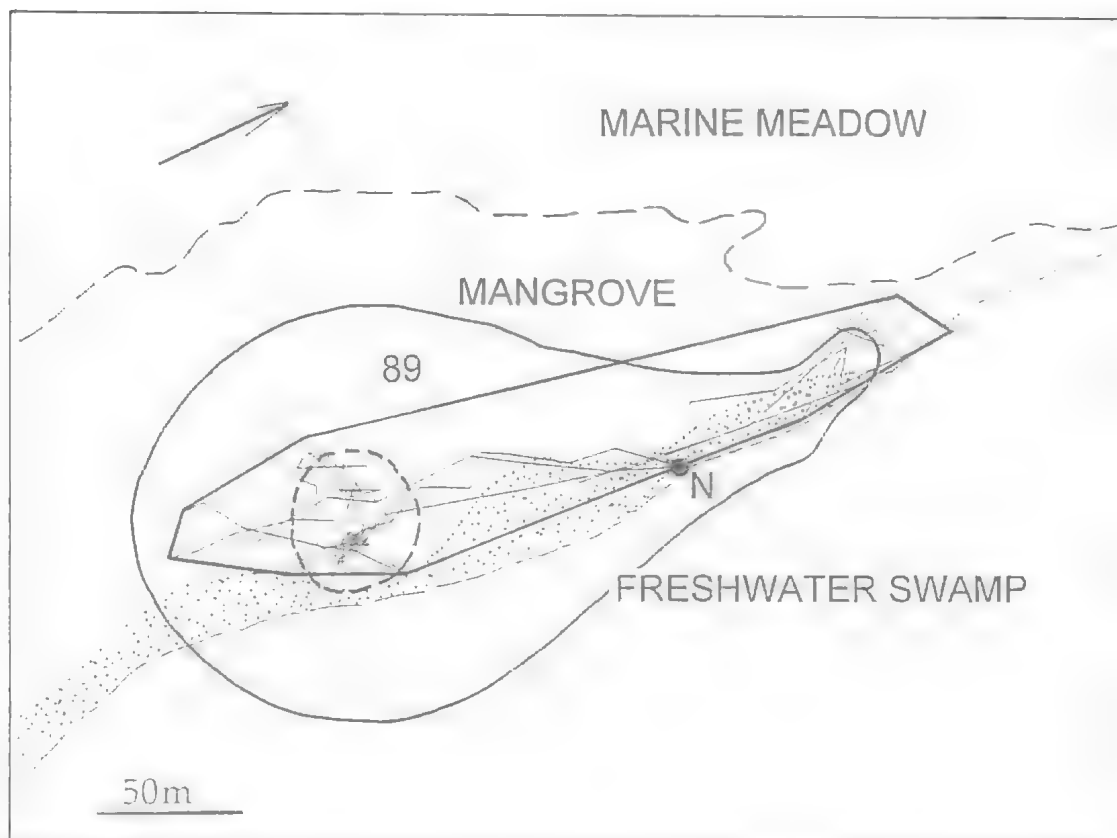


FIG. 21 Home range estimates (Harmonic Mean Measure – 95% isopleth [solid-line 'ellipse'] and 65% isopleth core area [broken-line 'circle'], Minimum Convex Polygon and actual trackway) recorded for adult male 89, Canalpin Creek (Site 5). Fine dotting denotes extensive area of shallow, brackish, stagnant lagoon. N denotes nest of AM89 in supralittoral bank. The arrow points north.

related terrestrial taxa, found semiaquatic species to converge morphologically in respect of the following suite of external and cranial attributes: 1, stiffer, more abundantly distributed mystacial vibrissae supported by thick mystacial pads; 2, reduced, incomplete or absent philtrum; 3, reduced and more densely furred pinnae; 4, hindfeet fringed with stiff, silvery hairs in plantar margins; 5, digits of hindfoot wholly or partly webbed; 6, round tails (in cross section) with longer, more dense ventral hairing; 7, metatarsal configuration approaching  $IV > III > II \geq V > I$ ; 8, large infraorbital foramen; and 9, large foramen magnum.

In *Xeromys myoides* the mystacial vibrissae are no more abundant and only marginally stiffer than in terrestrial species, but the mystacial pads are conspicuously thick, imparting a breadth to the muzzle belied (in the extracted skull) by a rostrum of average width. The philtrum is absent,

but the pinnae are not greatly reduced (average length 12.5mm), being clearly visible above the head, nor are they thickly furred. The hindfeet have no fringing hairs and they lack webbing, the tail is thinly and evenly furred dorsally and ventrally, and the metatarsal configuration ( $III > IV > II > V > I$ ) is that of terrestrial muroids (terrestrial soricids and *Microgale*). The foramen magnum in *Xeromys* is not especially enlarged (there is considerable cranial reduction in the vicinity of the cerebellum), and the same applies to the infraorbital foramen. However, the molar row is reduced to two per quarter, the eyes are small, the posture couchant, the fur water-repellent, and the upper incisors, as in ichthyomyines, approach an orthodont condition.

The modest degree of aquatic specialisation exhibited by *X. myoides* is remarkably convergent on that of the 54–61g African Brook Rat *Colomys goslingi*, which consumes mainly tri-



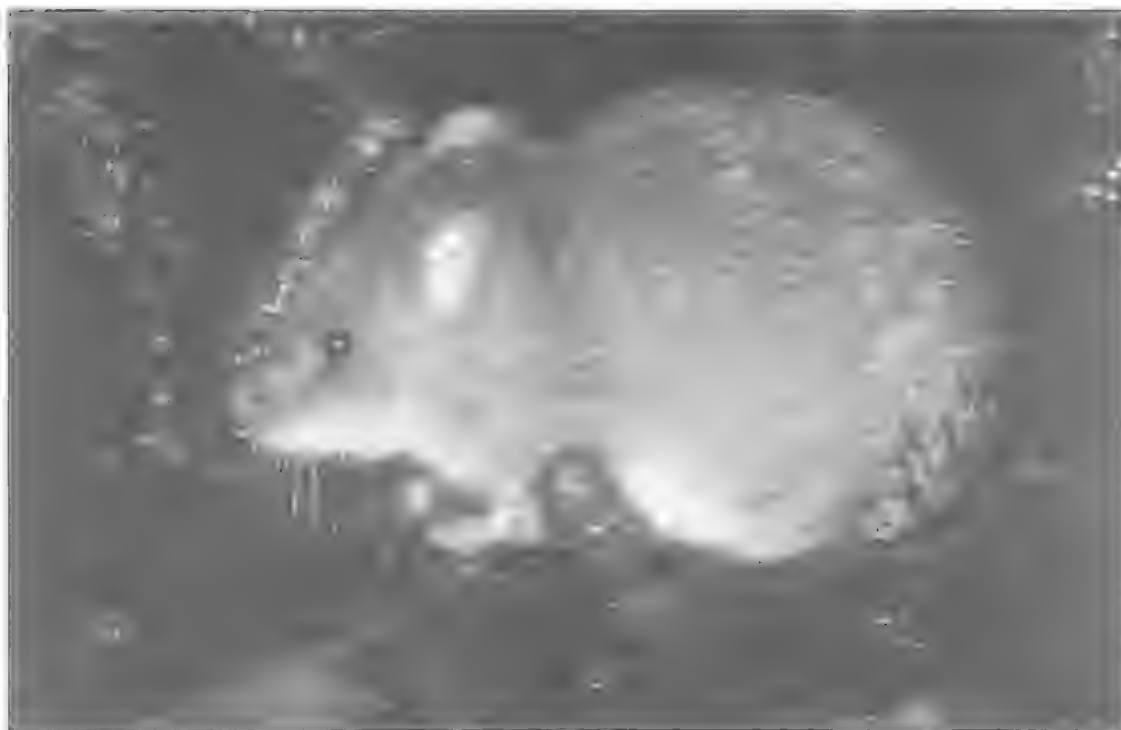


FIG. 22. Wild adult *Xeromys* shown in typical 'puddling' posture among pneumatophores. (Bruce Cowell).

chopteran larvae and terrestrial invertebrates in and adjacent to rainforest streams (Dieterlen, 1983). The reluctance of *Colomys* to enter deep water or to scale trees (Dieterlen, 1983) is also reminiscent of *Xeromys*. Other aspects of behaviour and ecology observed in the North Stradbroke study are consistent with the contention that *Xeromys* is an aquatic 'puddler' (Fig. 22) and not adapted to a truly semiaquatic lifestyle.

It is difficult to imagine what additional semiaquatic specialisation the littoral and supralittoral habitats might demand of *Xeromys*. Swimming adaptations, such as webbing of digits, fringing of lateral pes margins, elongation of lateral-most metatarsal proportions and development of a stiff ventral caudal brush, are clearly superfluous in a very small species to which deeper expanses of water must represent more of a risk of predation than an untapped resource (see Magnusson et al., 1976 for the record of *Xeromys* from a crocodile stomach). Similarly, stiffer, more abundantly distributed mystacial vibrissae are probably unnecessary given the species' observed preference for terrestrially acquired prey.

Observations of high daily food intake in captivity, rapid loss of body weight and ataxic behaviour associated with food deprivation, and

frenetic behaviour in the wild suggest a high metabolic level in the species. The very small size of *Xeromys* suggests that it might rapidly lose body heat through its relatively large surface area (compared to the volume of heat-producing tissue). This might be interpreted as particularly problematical for an animal continually in contact with water, especially as that small (vulnerable) body size may have already imposed a nocturnal life-style on the species.

However, the necessity to dissipate heat rather than the need to retain it may be the problem faced by *Xeromys*. Fanning & Dawson (1980) and Dawson & Fanning (1981) discuss the suggestion that many semiaquatic mammals have higher metabolic rates than those of similar-sized terrestrial mammals, their increased heat production compensating for losses to the aquatic environment. They conclude for the hypothermia-prone *H. chrysogaster* (Water Rat), that fur insulation (not tissue) is the major component of the rat's total insulation and that the ability of the fur to maintain an air layer between the skin and the water results in a significant retardation of the rate of heat loss.

There has been no published research to date on the insulative properties of the fur of *Xeromys*



although its water-repellent nature has been commented on by Watts & Aslin (1981) and Redhead & McKean (1975: 350) '... on leaving the water, *X. myoides* was dry; compared to *M. littoralis* which resembled the proverbial drowned rat'. The hair of *Xeromys* has been described as 'Pseudomys-like and unlike that of *H. chrysogaster*. It lacked 'shields' characteristics of other aquatic mammals and exhibited no structure known to impart water repellency' (B. Triggs pers. comm.). Despite its close association with an extremely wet, muddy habitat, and its tendency to sit, half-submerged, in small puddles for extended periods (Fig. 22), no examples of dirty, bedraggled or 'soggy' *Xeromys* were observed during the present study.

Dawson & Fanning's (1981) comments on the potential problems of heat loss faced by amphibious mammals when on land may have relevance to *Xeromys* if the water-repellent nature of its fur brings with it the associated cost of extra insulation. Given its avoidance of swimming, *Xeromys* may deal with the problem of heat dissipation by occupying saturated mud/peat/sand nesting mounds during the day and by 'puddling' while foraging at night (Fig. 22). In this respect it is difficult to deny an initial impression that the sparsely-haired tail and soft, near-naked, highly vascular pads of the hind feet of *X. myoides* represent surfaces evolved to dissipate heat. If this conjecture is correct, the southerly extent of distribution for this species might be determined not so much by thermoregulatory problems associated with decreasing ambient temperature and body heat loss, but by the decreasing abundance and diversity of suitable prey in less complex temperate mangrove forests (Clough, 1982; Hutchings & Saenger, 1987).

*Xeromys myoides* is a highly specialised terrestrial muroid rodent especially adapted to the littoral zone, one of the harshest of environments available to mammals. Its level of adaptation should not be regarded as an early stage of specialisation toward a more truly semiaquatic form, but a successful end product.

**STATUS.** *Xeromys myoides* has been described as 'one of the rarest of our native mammals' (Ride, 1970), 'vulnerable to changes caused by man' (Watts & Aslin, 1981), 'rare, scattered (probably at risk in some habitats and extinct in others)' (Redhead, 1983) and 'vulnerable' (Kennedy, 1990; Van Dyck, 1991). More recently it has been listed in the Rodent Action Plan with

nine other Australian rodents as 'rare or insufficiently known' (Lee, 1995).

This study has demonstrated that no special skill is required in capturing *X. myoides*, and it suggests that mangrove surveying elsewhere for *Xeromys* has probably been inadequate. However, the other possibility that North Stradbroke Island's fecund *X. myoides* population might represent the makings of an island remnant population such as that seen in *Leporillus conditor*, *Lagostrophus fasciatus*, *Setonix brachyurus* or *Bertongia lesueur*, should not be ignored. Given the proximity (200m) of areas such as Stockyard (southern North Stradbroke Island) to the complex mosaic of mangrove communities associated with lower Moreton Bay and the mainland, it seems likely that at the very least, the lower Moreton Bay islands should support populations of *X. myoides* similar to that of North Stradbroke. The number of mainland records also suggests that the rat is widespread and of reasonably broad habitat tolerance. However, until the North Stradbroke Island population is put into a broader mainland perspective the conservation status of *Xeromys myoides* will remain in question.

#### ACKNOWLEDGEMENTS

This study is dedicated to Ellie Durbidge who inspired and encouraged the research. I am most indebted to Judy Conrad and Barney Hines for all their help with the field and laboratory work associated with this project. On a voluntary basis Judy tirelessly assisted with translating thousands of flagging tape coordinates from mangrove trees to home range figures. Ellie and Tony Durbidge (Nth Stradbroke Is) provided accommodation, food, support and baby-sitting. Peter Bostock (Queensland Herbarium) provided plant identifications. John Bertram (Queensland University) identified injected plant material, Peter Davie and John Stanisic (both of Queensland Museum) identified crustacean and mollusc food scraps, and Rob Domrow (Queensland Museum) and David Kemp (CSIRO, Long Pocket) identified arachnid parasites. Consolidated Rutile Limited and Peter Foote provided access to Canalpin Ck. Field assistance or advice was made freely available by Ian Gynther (Queensland Department of Environment), Matthew Shaw and Heather Janetzki (Queensland Museum), Sally Townley (Southern Cross University), Anne-Marie Wall (Maleny), Bruce and Carolyn Cowell (Queensland Museum), Barbara Triggs (Genoa), David Titley (Titley Electronics, Ballina), Belinda Dett-

man and Lindsay Hardy (Australian Nature Conservation Agency). The endoscope and light source were generously supplied by medical specialists John Quayle and John Nye (both at Wickham Tce, Brisbane). Bruce Cowell (Queensland Museum) endured many sleepless nights for the sake of photography associated with this study. I gratefully acknowledge the help of all those listed above. I thank Gordon Guymer (Director, Queensland Herbarium, Dept of Environment) for permission to reproduce the maps of Dowling (1986). Ian Gynther (Queensland Dept of Environment), John Woinarski (Parks & Wildlife Commission of the Northern Territory) and John Seebeck (Dept of Conservation and Natural Resources, Victoria) are especially thanked for their critical input into drafts of this paper.

The Endangered Species Program (Australian Nature Conservation Agency) is thanked for providing much of the funding associated with this research.

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THE NEW HOLLAND MOUSE *PSEUDOMYS NOVAEHOLLANDIAE* (RODENTIA: MURIDAE), AN ADDITION TO THE MAMMAL FAUNA OF QUEENSLAND

STEVE VAN DYCK AND BRUCE LAWRIE

Van Dyck, S. & Lawrie, B. 1997 06 30: The New Holland Mouse *Pseudomys novaehollandiae* (Rodentia: Muridae), an addition to the mammal fauna of Queensland. *Memoirs of the Queensland Museum* 42(1): 367-376. Brisbane. ISSN 0079-8835.

The New Holland Mouse *Pseudomys novaehollandiae* (Waterhouse, 1843) is reported for the first time from Queensland where an adult male was collected at Crows Nest (near Toowoomba) in open forest. The capture site contrasted markedly with published records of southern *P. novaehollandiae* habitat in its relatively high altitude (560m), distance from the coast (100km), total lack of a dense shrub layer, and advanced seral stage. However, examination of unpublished trapping records from northern New South Wales suggests that at the northern limit of its range these environmental features may not be exceptional. □  
*Rodentia, Muridae, Pseudomys novaehollandiae, Queensland*

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Thirty years ago the New Holland Mouse *Pseudomys novaehollandiae* (Waterhouse, 1843) was believed extinct or extremely rare in Australia. At that time, given its remarkably obscure status since description in 1843, few would have cared. However, in 1967 it was rediscovered alive at Port Stephens (Keith & Calaby, 1968) and at Ku-ring-gai Chase National Park in New South Wales (Mahoney & Marlow, 1968). Three years later it was recorded from Victoria (Seebeck & Beste, 1970) and then, in 1975, discovered in Tasmania (Hocking, 1980). Since then it has been recorded from widely scattered east-coastal localities between Evans Head (29°07'32"S 153°26'31"E) in New South Wales (Posamentier & Recher, 1974), and Friendly Beaches (42°00'S 148°17'E), Tasmania (Hocking, 1980). In New South Wales its legal status is 'protected', but the species is now the object of considerable conservation concern in Victoria (Wilson, 1993, 1996), where it is regarded as 'endangered' and listed under the Fauna and Flora Guarantee Act 1988.

In New South Wales *P. novaehollandiae* has been recorded in the literature from dry sclerophyll forest associated with a dense shrub layer on dune sands (Keith & Calaby, 1968; Batt et al., 1972), from around the edges of sedged freshwater swamps between dunes (Keith & Calaby, 1968), and from coastal heaths (Posamentier & Recher, 1974; Fox & Fox, 1978). Its occurrence in heath regenerating after sand mining is documented by Fox & Fox (1984). In Victoria it has been trapped in open dry sclerophyll forest (Seebeck & Beste, 1970), woodland and low-open forest with a heathy understorey (Kentish,

1981; Wilson, 1994, 1996), low dense heath (Gilmore, 1977; Braithwaite & Gullan, 1978; Norris et al., 1983; Opie, 1983; Wilson, 1991, 1996), and primary sand dunes with tussocks and sedges or dune scrub with sedges and low shrubs (Quin, 1994; Menkhorst, 1995; Wilson, 1996). Menkhorst (1995) considered optimum Victorian habitat to be seral stages of dry heath. In Tasmania *P. novaehollandiae* has been found in the woodland/heath mosaics of the coastal northeast. The generally accepted importance of early successional vegetation (3-4 years) to this species is discussed by Wilson (1994, 1996).

Relatively recent trapping records from northern New South Wales suggest that the habitat prescription usually associated with *P. novaehollandiae* needs modification. Our report here, of the discovery of the species in Queensland, 100km from the coast and at over 500m elevation, is one of a number of records suggesting this is not atypical for the New Holland Mouse in the north.

## THE DISCOVERY

In late August 1996, 12 small Elliott mammal traps baited with bread and jam were set (B.L.) in open forest adjacent to the family home overlooking the township of Crows Nest, 32km north of Toowoomba, southeast Queensland (Fig. 1). The simple trapping exercise was part of field experience for a girls' group staying with the family overnight. Next morning the traps were found to contain 3 House Mice and 2 unfamiliar mice suspected to be Delicate Mice *Pseudomys*

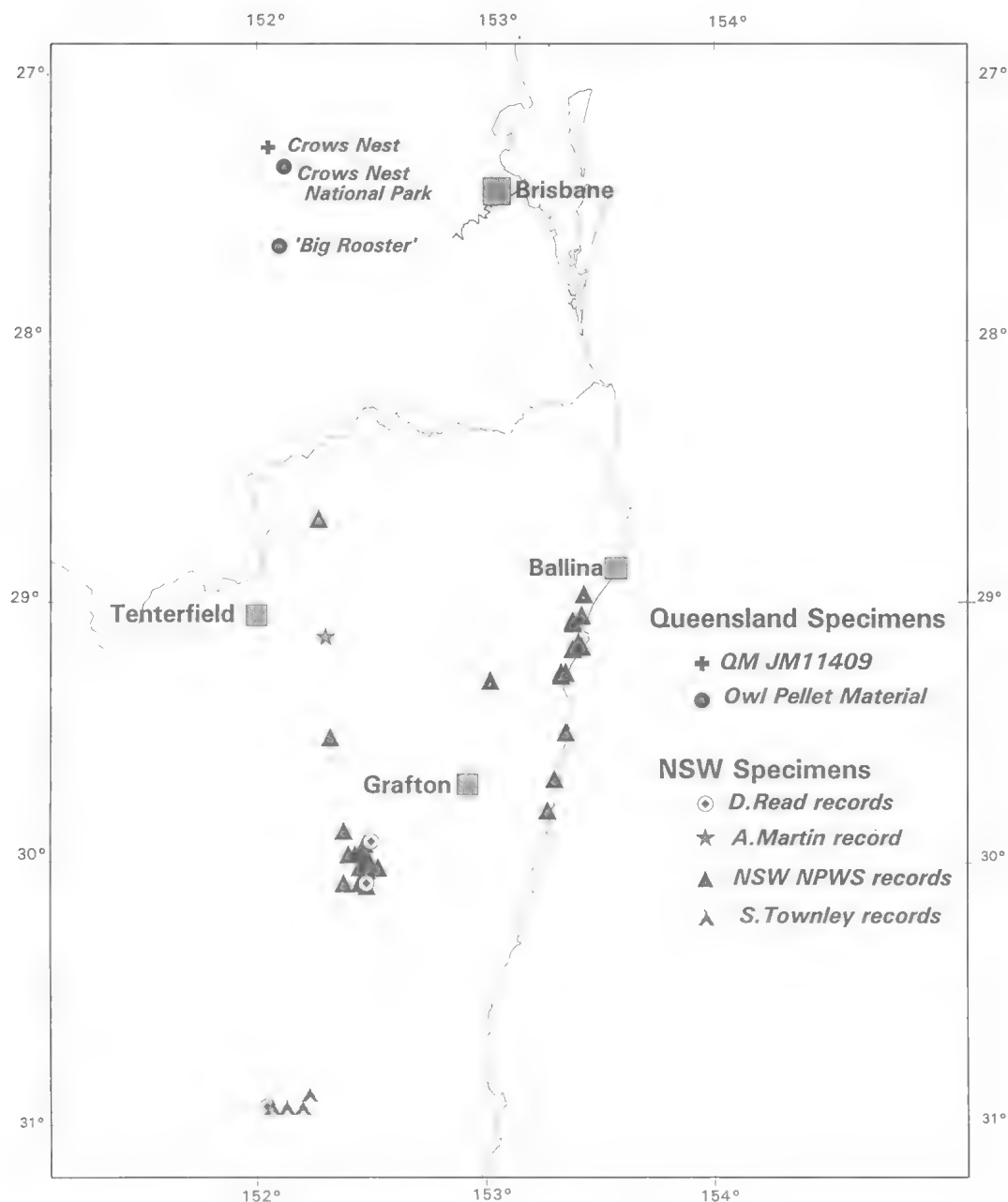


FIG. 1. Collection sites of live *Pseudomys novaehollandiae* and owl pellet material from south-east Queensland, with recent trapping records for northern New South Wales.

*delicatulus*. One was sent live to the Queensland Museum and the other was released at the capture site. The animal was photographed (Fig. 2) and registered in the Queensland Museum mammal collection as QM JM11409. In assigning an iden-

tity to this specimen, it was compared in particular against type material representing *P. pilligaensis* (see Fox & Briscoe, 1980). The relatively broader rostrum, broader interorbital width, narrower palate and incisive foramen, and relatively

smaller bullae of the Crows Nest specimen collectively suggested its affinities lay with *P. novaehollandiae* and not with *P. pilligaensis*. Analysis of hair samples (B. Triggs pers. comm.) and features of external morphology (B. Wilson pers. comm.) also confirmed the identity of JM11409 as *P. novaehollandiae*.

Since capture of JM11409, trapping (B.L.) at Perseverance section of Crows Nest National Park 453 (150 trap nights), Bungaree section of Crows Nest National Park 453 (150 trap nights), and at, or adjacent to, the original capture site (305 trap nights) has failed to secure more examples of this species.

### DESCRIPTION OF CAPTURE SITE

JM11409 (and the released specimen) were caught in tall open forest (27°15'09"S 152°03'22"E), 1km north of Crows Nest. The capture site (Figs 3 & 4) at 560-570m above (mean) sea level (a.s.l.) abuts the town's cemetery.

**TOPOGRAPHY AND SOIL.** Crows Nest, 100km northwest of Brisbane, is situated on the eastern edge of the Great Dividing Range virtually overlooking Esk in the Brisbane Valley. The Crows Nest Shire's northern boundary is formed by the northeast-southwest-aligned Blackbutt Range which joins the Great Dividing Range at the north-west boundary. Average elevation throughout the Shire is 575m a.s.l., the lowest point in the Shire is Maronghi Creek at around 150m, and the highest, Mt Perseverance at 807m. Topography throughout is mainly undulating; rolling hills to the west and steeply sloping ranges and escarpments to the east. Geology of the area has been mapped by Cranfield & Schwartzbock (1973). Soils throughout are mainly hard-setting loams to clay loams overlying yellowish-grey clay subsoils (solodized solonetz/solodics), deep sands (siliceous sands), reddish-brown clay loams overlying red and brown clays (red-brown earths and yellow earths) and shallow, stony sands and loams (lithosols). Surface soil texture is coarse or clay-loam, and sand is commonly present on the surface. Coarse-grained sediments of the Marburg Formation, Woogaroo Subgroup and Tarong Beds form the parent material. Soils of the general capture area are massive and cross-bedded siliceous sandstone, some conglomerate, minor siltstone and shale. Surface soil in the open forest of the immediate capture area was dark friable clay-loam without sand.

**CLIMATE.** Annual rainfall in the Shire ranges from 650mm to 1200mm. The collection site receives average annual rainfall of between 750 and 950mm distributed unevenly throughout the year. The dry season months (between April and September) receive average monthly falls of around 50mm whereas the summer months of January and February average around 125mm. Temperature and humidity records are similar to those for Toowoomba (32km south) where daily mean maxima are around 27°C for January/February and 17°C for June/July, with daily mean minima of 17°C for January/February, 6°C for June/July. On average, temperatures exceed 32°C on ten days of the year and frosts occur between May and September. Average humidity is highest February to July (68%) and lowest in September (54%).

**VEGETATION.** Vegetation at the capture site was tall open-forest. Dominant species of the upper stratum (18-19m with 60% projected foliage cover) were *Angophora leiocarpa* (common [C]), brown bloodwood *Corymbia trachyphloia* (C), yellow stringy bark *Eucalyptus acmenoides* (C), Helidon ironbark *E. taurina* (sub-dominant and uncommon [U]) and grey gum *E. major* (C), all to a maximum circumference at breast-height (CBH) of 2m. A very sparse midstorey (6-7m with 8% cover) was composed of curracabah *Acacia concurrens* (C), lightwood *A. implexa* (U), Queensland silver wattle *A. podalyriifolia* to 2m (U), rose sheoak *Allocasuarina torulosa* (C), kurrajong *Brachychiton populneus* subsp. *trilobus* to 3m (rare [R]) and *Lophostemon suaveolens* (U). A low, open understorey (75% cover) consisted of the following: *Paspalidium* sp. to 40cm (C), *Patersonia sericea* to 50cm (C), white root *Lobelia purpurascens* (C), *Hardenbergia violacea* (U), *Laxmannia gracilis* to 25cm (R), coffee bush *Breynia oblongifolia* (R), wiry panic *Entolasia stricta* to 30cm (Abundant [A]), many flowered matrush *Lomandra multiflora* (R), matrush *L. filiformis* to 30cm (A), blue flax lily *Dianella caerulea* (R), tall spear grass *Austrostipa pubescens* in patches up to 5m diameter to 1.5m high, variable sword edge *Lepidosperma laterale* to 60cm (C), blady grass *Imperata cylindrica* in patches, to 50cm, barbed wire grass *Cymbopogon refractus* to 1m (when seeding) (A), *Solanum nemophilum* to 50cm (A), bower plant *Pandorea jasminoides* (U), monkey rope *Parsonia straminea* climbing to 8m (R), *Acrotriche aggregata* to 2m (A), lady's slipper *Hybanthus monopetalus* to 30cm (U), *Calotis cuneifolius* (R), *C. cannifolia* to 20cm (R), *Jack-*

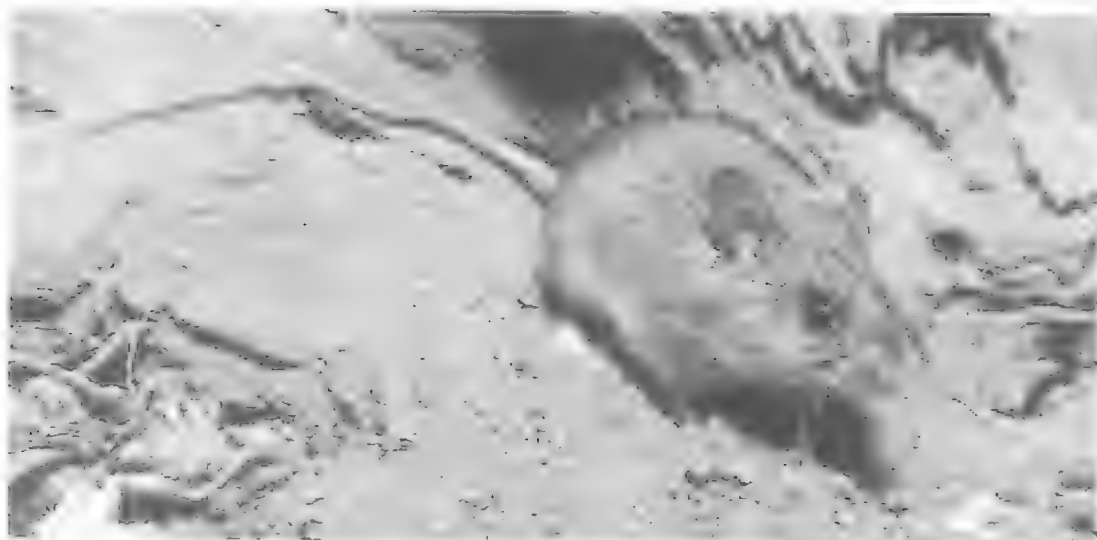


FIG. 2. Adult male *Pseudomys novahollandiae* QMJM11409 from Crows Nest, southeast Queensland.



FIG. 3. Capture site of QMJM11409, Crows Nest, showing low, open understorey.





*sonia scoparia* to 3m (C), *Leucopogon muticus* to 1.5m (U), *Melichrus urceolatus* to 30cm (U), *Goodenia rotundifolia* (A), *Canthium buxifolium* (R), *Maytenus silvestris* to 50cm (C), *Pomax umbellata* to 10cm (C), *Desmodium rhytidophyllum* to 30cm (U), *Grevillea* sp. to 2m (R), and unidentified grasses. It was thickly littered with dead leaves, sticks, fallen trunks and branches.

Approximately 200m east of the collection site, sandstone outcrops and boulders along an ephemer-

eral creek became conspicuous and marked a dramatic change in the botanical composition of the understorey and ground layer (Fig. 5). Dominant species of the upper stratum (13m with 50% projected foliage cover) were *Angophora* sp. (A), brown bloodwood *Corymbia trachyphloia* (U) and yellow stringy bark *Eucalyptus acmenoides* (A) to a maximum CBH of 3.35m.

The understorey changed to a dense species-rich heath dominated by *Xanthorrhoea johnsonii*



to 2.3m (A). Around the creek, foliage cover reached 80-90%, in other areas this reduced to 10% with virtual monocultures of *X. johnsonii*. Other heath understorey species included *Leptospermum polygalifolium* to 2.5m (C), *Banksia spinulosa* var. *collina* to 1.2m (C), *Leucopogon muticus* to 2m (U), and *Hakea eriantha* to 1.8m in patches. The shrub layer consisted of *Persoonia sericea* to 80cm (C), *Notelaea linearis* along the heath edge to 2m (C), *Jacksonia scoparia* to 2m (U), *Mirbelia speciosa* subsp. *ringrosei* to 80cm (C), *Hibbertia stricta*, *Stylidium laricifolium* to 60cm in patches, *Melichrus urceolatus* to 40cm (U), *Acrotriche aggregata* to 80cm (U), *Hibbertia linearis* var. *obtusifolium* (U), *Acacia podalyriifolia* along heath edge to 2.1m (U), *Pomax umbellata* 10cm (C), shorthair plumegrass *Dichelachne micrantha* to 30cm (C), *Lepidosperma laterale* to 40cm (C), *Austrostipa pubescens* in patches to 1.5m, rock fern *Cheilanthes sieberi* (R), *Entolasia stricta* to 80cm (A), *Paspalidium albobilosum* to 80cm (C), *Ozothamnus diosmifolius* (R), *Poranthera microphylla* to 8cm (R), *Pimelea linifolia* to 50cm (U), wiry panic *Entolasia stricta* to 80cm (A), and many unidentified grasses. A thick ground layer consisted of fallen sticks, leaf litter, bark shreds, rocks, logs and an abundance of *Angophora* sp. seed capsules.

Apart from the occasional stray, the collection site is not grazed by cattle, and fire may have been absent from the area for 30 years or more. Unburnt skirts on 2m-high *Xanthorrhoea* individuals were noted almost touching the ground.

### THE ANIMAL

Adult male *P. novaehollandiae* JM11409 (Fig. 2) is compared in Table 1 with measurements from a wide range of adult males collected in the Port Stephens area by Keith & Calaby (1968). While the Port Stephens specimens weighed 13-18g (collected in February) and JM11409 weighed slightly less at 12g (collected August) most measurements suggest that, in comparison, the Queensland specimen is a small animal. However, the more commensurate molar measures, and relative lack of molar wear, suggest that the Crows Nest mouse may still have been growing.

### DISCUSSION

The suspicion that living *P. novaehollandiae* might occur in Queensland was first aroused in 1993 when Veronica Hinman (University of Queensland) analysed unregistered regurgitated

owl pellet material stored in the Queensland Museum. She attributed fragmentary remains from three southeast Queensland sites to *P. novaehollandiae* (Hinman, 1993). These sites were 1, 'Big Rooster Cave' near Gatton (material excavated by H. Godthelp in June 1982); 2, Perseverance section of Crows Nest National Park (material collected by David Read in May, June 1988); and 3, Cania Gorge (material collected by Mary Wade in 1978). Confirmation of the identity of the Gatton and Cania Gorge fragments was sought from Alex Baynes (Western Australian Museum) who attributed the nine Cania Gorge dentaries to an unknown pebble-mound mouse (now known to be *Pseudomys patrius*, S.V.D. unpublished data). But he was reluctant to assign an identity to the maxillary fragments from the Gatton individual (QM JM10306), its broad, more rounded molars and the unusual relationship between adjacent cusps on M<sup>2</sup> and M<sup>3</sup> being unlike his comparative material of *P. novaehollandiae* from Smith's Lake, New South Wales. Given this finding, the more incomplete Crows Nest National Park fragments (dentaries and maxillary fragments of one individual QM JM10304) were temporarily shelved.

More recent comparison with Victorian specimens (Museum of Victoria C26607, C22127, C10348, C16047) now suggests that the Gatton specimen is, after all, attributable to a large, old individual of *P. novaehollandiae*, and reappraisal of the Crows Nest National Park fragments confirms Hinman's assessment that Read's owl pellets contained a New Holland Mouse. Read's effort of 600 trap nights between 24 May-1 June 1988 in the Crows Nest National Park resulted in no mammal captures (Read, 1988a) but his owl pellet material contained examples of *Rattus lutreolus*, *R. tunneyi*, *P. gracilicaudatus*, *Sminthopsis murina*, *Perameles nasuta*, *Petaurus breviceps* and *Pseudocheirus peregrinus* all of which are registered in the Queensland Museum mammal collection.

'Big Rooster' (south of Gatton) and Crows Nest National Park are approximately 65km S and 5km E, respectively, of the capture site of JM11409. In Crows Nest National Park, Read collected the owl pellets from three caves in the rocky cliffs (around 27°19'S 152°07'E) overlooking Perseverance Creek (Read, 1988a). Godthelp collected the 'Big Rooster' material from a rock shelter in eucalypt forest surrounded by open woodland and degraded grazing country (the exact coordinates of 'Big Rooster' cave have not yet been established but are thought to be

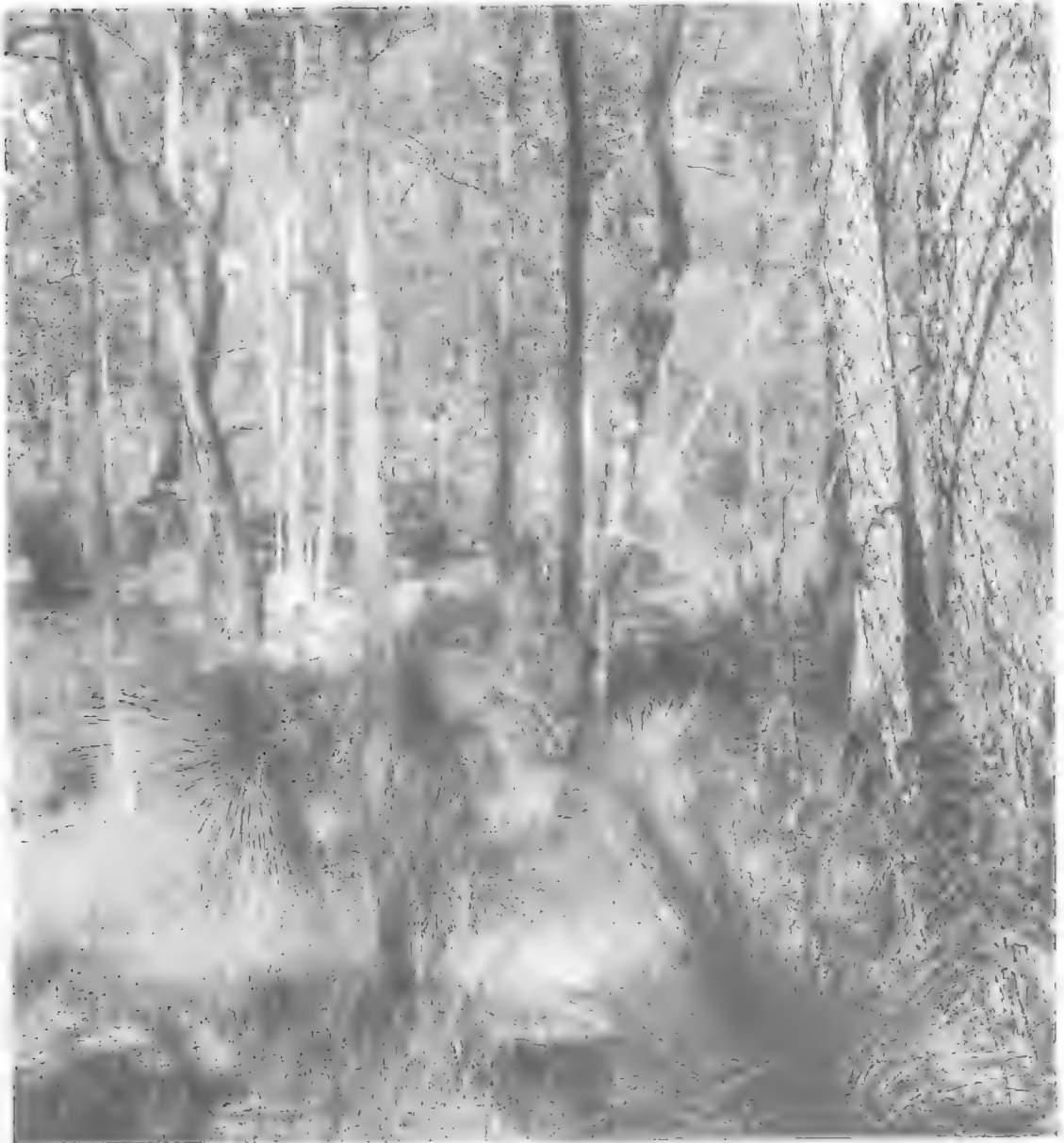


FIG. 5. Heath adjacent to Crows Nest capture site.

around 27°38'S 152°06'E). Trapping (unsuccessful) for living *P. novaehollandiae* has since been conducted in Perseverance section of Crows Nest National Park, but other sites are yet to be surveyed.

Initially, the collection site of JM11409 appeared atypical for *P. novaehollandiae* in its relatively high altitude, distance from the coast, lack of a dense shrub layer, and advanced seral stage. It seemed as far removed from the optimum hab-

itat proposed by Posamentier & Recher (1974) (heath, actively regenerating from fire) as it was from those habitats occupied in Victoria and New South Wales (see Wilson, 1994). However, the distance from Crows Nest to the coast (100km) is actually exceeded by the distance (166km) from the type locality (Yarrandi, near Scone, New South Wales), to the coast. Nearby collection sites at Belltrees (31°59'S 151°08'E, Kemper, 1977) and further east near Barrington Tops (1976 record

TABLE 1. Comparison of Queensland (Crows Nest) specimen QM JM11409 against a Port Stephens (NSW) series of males ( $\geq 13$ g) (from Keith & Calaby, 1968). Weight expressed in grams, all other measurements in millimetres. For method of measurement see Taylor et al. (1982).

Measurement	QMJM 11409	Port Stephens series		
		No.	Range	Mean
Weight	12	19	13-18	14
Head-body	78.7	19	78-85	84
Tail	76.5	17	86-101	93
Pes	18.7	19	20.5-22	21
Ear	14.4	19	15.5-17	16
Skull length (occipitonasal)	22.8	18	23.1-25.1	24.2
Condylbasal length	20.7	19	21.1-22.5	21.9
Basal length	18.6	19	19.1-20.8	20.0
Zygomatic width	11.5	19	11.5-12.7	11.9
Interorbital width	3.6	19	3.5-4.1	3.8
Interparietal length	2.5	18	2.9-3.8	3.4
Interparietal width	7.2	19	7.3-8.3	7.7
Braincase width	11.0	19	11.1-12.0	11.5
Mastoid width	9.3	19	9.3-10.8	9.9
Nasal length	8.4	18	7.8-9.4	8.6
Nasals width	2.2	17	2.2-2.6	2.4
Palatal length	11.0	19	11.6-12.9	12.3
L. palatal foramen length	4.9	19	4.5-5.4	4.9
Palatal foramina width	1.6	19	1.2-1.8	1.5
Inside $M^{1-1}$ width	2.2	19	2.3-2.7	2.5
Outside $M^{1-1}$ width	4.6	19	4.8-5.3	5.0
Bulla length	5.0	19	4.2-4.9	4.5
Crowns $M^{1-3}$ length	3.4	19	3.5-3.8	3.6
Alveolar $M^{1-3}$ length	3.8	19	3.7-4.0	3.8
Crowns $M^{1-2}$ length	2.9	19	2.5-2.8	2.7

from New South Wales National Parks and Wildlife database) are additional examples of *P. novaehollandiae* habitat situated far from the coast. Although Yarrandi, Belltrees and Barrington Tops are approximately 520km south of Crows Nest, all three collection sites are structurally reminiscent of the Crows Nest site (B. Fox pers. comm.). Furthermore, examination of unpublished reports and relatively recent trapping records suggest that around the northern limits of its range, high altitude and low longitude are regularly encountered features of the *P. novaehollandiae* profile.

Read (1988b) trapped one specimen at 30°05'12"S 152°28'59"E in Marengo State Forest (60km southwest of Grafton, NSW) in 1987, at an altitude of 650m. In August 1992 he trapped a single specimen in the Carai State Forest (inland from Port Macquarie) (Read, 1995), at

30°55'39"S 152°05'19"E and around 860m (D. Read pers. comm.). In September 1993, Sally Townley trapped six individuals on Carai Plateau, at 30°52'59"S 152°14'14"E, and an altitude of 900m. Here, the site was open forest of mainly *E. laevopinea* with an understorey dominated by *Lomandra* sp. (S. Townley pers. comm.). Both Read and Townley have trapped *P. novaehollandiae* in Chaelundi State Forest. In March 1991 Read caught an individual at 29°55'S 152°30'E on grass-covered alluvium with an *E. tereticornis* overstorey (Read, 1993). In October 1993, Townley caught several animals at 30°01'21"S 152°29'46"E at an altitude of 840m. The forest type was New England blackbutt *E. campanulata*, grey gum *E. propinqua*, yellow stringy bark *E. acmenoides*, blue gum *E. saligna* and tallow-wood *E. microcorys* with an understorey of shrubs, grasses and small herbs (Townley, 1993). More recently, over 20 individuals of *P. novaehollandiae* were trapped by Townley at a number of sites in Oxley Wild Rivers National Park (southeast of Armidale) around 30°55-56'S 152°04-12'E, along an altitudinal gradient from about 400-1000m. Trapping sites supported various types of open forest with overstorey trees including New England blackbutt, grey box, Blakely's red gum *E. blakelyi*, blue gum and grey gum. Some sites had grassy understoreys and others had a dense heath layer (S. Townley, pers. comm.).

Closer to the Queensland border, one specimen has been trapped at around 900m a.s.l. on Timbarra Plateau, 29°07'38"S 152°18'22"E, east of Tenterfield, in forest dominated by New England blackbutt and *E. olida*, with a heathy understorey (Martin, 1995). New South Wales National Parks and Wildlife database records document a 1987 record of *P. novaehollandiae* as far north as 28°41'S 152°16'E (southeast of Lindsay View) at around 828m. This, and other most northerly records from that database appear with the Read, Townley and Queensland records in Fig. 1.

All these records confirm both the regular occurrence of *P. novaehollandiae* at high altitudes, and the use of tall open-forest at low latitudes. Some of the records confirm its presence in grassy understoreys. However, the proximity of grassy understorey to heath (or other forms of dense understorey) should be examined before attributing grass as a preferred habitat to the species. For example, the Crows Nest capture site was 182m away from an adjacent area of species-rich, densely shrubbed (but dry) heath. While

Kemper (1977) reported an order of habitat preference in *P. novaehollandiae* from heath to open forest regenerating after recent burning. Fox & McKay (1981) showed that the habitat requirements of the species were most likely contained completely within the shrub layer of heath-type species with the presence or absence of trees unimportant. More recently Fox (1996), re-confirmed *P. novaehollandiae* as a species selecting bare ground and vegetation open to a height of 20cm (typical of the early seral stages). But, he showed that although in open forest its maximum abundance occurs around 1.5 years after burning (followed by decreased abundance), it re-peaked in abundance around 16 years after the initial burn, by which time the understorey was open to around 2m above the ground. In heath, similar peaks occurred at 3 and 13 years following fire.

Male JM11409 (weighing 12g at capture in August) may have been relatively young at the time of capture. Kemper (1980) recorded sexually mature and immature males from mid-coastal New South Wales at mean weights of 14.3g and 12.9g respectively. One third of males in her study achieved sexual maturity in the breeding season of their birth (August to January, and occasionally to March). That the Crows Nest male JM11409 was still growing, is made more plausible by the recent extension of the *P. novaehollandiae* breeding season (in New South Wales) to late July (Fox, Higgs & Luo, 1993). Although trapped in an open grassy understorey, male JM11409, if still relatively young, might not have been residing in the area, but dispersing through it.

The contemporaneous coastal occurrence of the New Holland Mouse at low latitude near Evans Head (29°07'32"S 153°26'31"E) demonstrates that in the north, habitat parameters are much broader than those previously ascribed to the species. Indeed, there seems little reason to doubt that it should also occur in coastal Queensland. Habitat resembling that utilised by *P. novaehollandiae* in Victoria and New South Wales would appear to occur in coastal and off-shore southeastern Queensland heaths and sedged dunes, particularly in localities such as Coolangatta, North and South Stradbroke Islands, Moreton Is and the Great Sandy Region.

Ironically, the following comment made by Keith and Calaby soon after *P. novaehollandiae* was rediscovered alive in New South Wales has not yet outlived its pertinence 30 years on: 'This discovery of a populous colony of the New Holland mouse in an area close to urban settlement

and industrial development is an indication of our lack of knowledge of the abundance and distribution of at least some members of the indigenous fauna' (Keith & Calaby, 1968: 58).

#### ACKNOWLEDGEMENTS

We thank Rick Galbraith (Crows Nest Shire Council) for supplying physical feature descriptions of the Shire, Rodney Hancock and Errol Ryan (Queensland Department of Environment) for advice on vegetation community distribution and field trapping sites in Crows Nest National Park. Heather Janetzki (Queensland Museum) prepared the map, and along with Marion van der Donk (Queensland Museum), assisted with collection and preparation of botanical specimens. We gratefully acknowledge the help of Alexander Baynes (Western Australian Museum), Barbara Triggs (Genoa) and Barbara Wilson (Deakin University), and thank Lina Frigo (Museum of Victoria) and Tish Ennis (Australian Museum) for lending us specimens in their care. Tim Kingston (Queen Victoria Museum, Launceston) and Deyarne Plowman (New South Wales National Parks and Wildlife Service) kindly supplied their data records. Bruce Cowell (Queensland Museum) photographed the animal and habitat featured in this paper. We particularly acknowledge Gordon Guymer, Rebecca Francis and Rod Fensham (Queensland Department of Environment, Queensland Herbarium) for identifying botanical specimens, Sally Townley (Southern Cross University) and David Read (Mount King Ecological Surveys) for allowing us to use their unpublished trapping records, and Ian Gynther (Queensland Department of Environment) and Barry Fox (University of New South Wales) for many helpful comments and discussions during preparation of this manuscript.

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**OBITUARY: CHARLES TANNER, HERPETOLOGIST.** *Memoirs of the Queensland Museum* 42(1): 377. 1997. Conversations with herpetologists suggest that some of us are 'born' and some are 'made'. Charles Tanner (born 19 January, 1911, Brighton, England; died 23 December, 1996, Cairns, Australia) was definitely one of the former. Amongst his earliest memories were those of days spent 'haunting' the reptile house of London Zoo. Wherever he was — the United Kingdom, Iraq (Abadan), Palestine, Cyprus, the United States of America, Papua New Guinea, or Australia (from Tasmania to Cape York and Byron Bay to Carnarvon) — he observed, admired, photographed and collected reptiles, and wrote and talked about them. They were a life-long obsession.

Charles Tanner's contributions to knowledge of Australia's reptiles were substantial. He had long affiliations with the Museum of Victoria, Melbourne, and the Queensland Museum, Brisbane. He was an Honorary Associate of the latter from 1953 until his death. His collections for that museum included 522 frog and 573 reptile specimens. Many of these were collected on his annual leave. Each year, for many years, he and one of us (AJC) travelled to herpetologically unknown or poorly known sites, Australia-wide. His knowledge of, and enthusiasm for finding frogs and reptiles was a never-ending source of astonishment. In 1955, he and Charles Brazenor (then Assistant Director of the MOV), collected the first specimens of *Philonia frosti* Spencer 1901 (a rare frog, narrowly confined to Mt Baw Baw, Victoria) seen since collection of the holotype of the species. On New Year Island, Bass Strait, in 1953 and 1954, he photographed Black Tiger Snake, *Notechus ater*, and Shearwater, *Puffinus tenuirostris* interactions. Only one of these photographs has been published (Worrell, 1963). The rest are now part of his estate, hopefully to be lodged in a museum for posterity.

His association with the Queensland Museum began in 1968. His last donations were made in 1990. Between 1968 and 1990, Charles Tanner donated 302 frog, 548 reptile and 42 mammal specimens to the Queensland Museum. Amongst them are type specimens on which descriptions of many new species were based: *Cophixalus saxatilis* Zweifel & Parker, 1977; *Curliu dogare* Covacevich & Ingram, 1975; *C. jarnoldae* Covacevich & Ingram, 1975; *C. scirtetis* Ingram & Covacevich, 1980; *Ctenotus astoric* Czechura, 1986; *C. nullum* Ingram & Czechura, 1990; *Cryptoblepharus johni*, Ingram & Covacevich, 1978; *Leisania ingrami* Storr, 1991; and *Leggadina lakedownensis* Watts, 1976 (possibly a junior synonym of *L. forresti*). Tanner's special interests lay not in description and nomenclature, which he was content to leave to others, but discovering new taxa. Recognition of a new

species, collection of specimens, their careful preservation and lodgement in a museum were the parts of a taxonomist's job that he relished. Through this, he encouraged the work and careers of several taxonomists.

Elapids dominated Tanner's research interests and, to a certain extent, his life. For many years he kept a wide range of species as treasured 'pets'. Between the early 1960s and 1985, he 'milked' specimens in his collection daily on behalf of the Commonwealth Serum Laboratories (now CSL Ltd), Melbourne, the sole producer of antivenoms in Australia from his dried venom supplies was made much of the antivenom produced in Australia. Many of the survivors of potentially life-threatening envenomations in Tanner's 'production time' owe their lives, in no small part, to work conducted at his snake farm-laboratory near Cooktown. His venoms were always of the highest quality and were used also in many research projects. His collaborations with Allen Broad of CSL were especially rewarding. The most exciting venom studied was that of *Oxyuranus microlepidotus*. In 1979 this venom was shown to be the most toxic snake venom in the world. Further investigations showed that it was neutralised effectively by existing Taipan (*Oxyuranus scutellatus*) anti-venom (Sutherland et al., 1978; Broad et al., 1979a,b). Venoms collected by Charles Tanner now form a valuable part of the National Collection of Venoms held by the Australian Venom Research Unit of the Department of Pharmacology, The University of Melbourne.

Many of his captive snakes had long and very productive lives in and, sometimes, on! his hands. Tanner survived many life-threatening bites. About them he was reluctant to talk, unlike many victims of snakebite (Pearm, 1990; Pearm et al., 1994). He invariably regarded herpetologists bitten as silly, not brave. 'Aggression is not a word I would apply to any snake...', he would say. In 1979, following massive envenomation by a Taipan (*Oxyuranus scutellatus*), Tanner was fortunate to receive the full premedication recommended by CSL. The infusion of antivenom was uneventful and the patient described as miraculous the return of strength in his limbs and the disappearance of his severe headache. 'Life mother's milk' was his description of his therapy. Steroid therapy followed for the next four days, because of his special vulnerability to delayed serum sickness. Tanner recovered uneventfully.

Charles Tanner's expert elapid husbandry involved the design and development of several 'safe' methods and tools of trade, all of which are still in use by those who follow him. Amongst these are the 'potato-masher' jigger and the hoop-bags of plastic and calico for 'tailing' specimens of several species, including Taipans; hide boxes with trap doors; and the use of strong, opaque plastic bag from which the largest elapid could be milked with relative safety. All minimised discomfort for the snake and maximised safety for the handler.

Tanner figured in the immunological literature as a result of his work with the large elapids. Following many bites, he had become highly allergic to CSL antivenom. For this reason, Dr Saul Wiener undertook active immunisation of Tanner with Tiger Snake (*Notechus scutatus*) venom in 1959. Wiener (1960) successfully immunised Charles Tanner through 24 injections of Tiger Snake venom over 13 months. This protection was transitory. Thereafter, Tanner rightly became apprehensive about antivenom therapy.

All elapids intrigued Tanner, but Taipans, *Oxyuranus* spp., intrigued him most. Perhaps his greatest excitement and contribution was catching the first live specimen seen by researchers of the snake now known as the Western Taipan, *Oxyuranus microlepidotus* (McCoy, 1879). Soon after his close association with the Museum of Victoria began, he read the description (1879) of *Diemenia macrolepidota* and examined the two type specimens of this species in the (then)

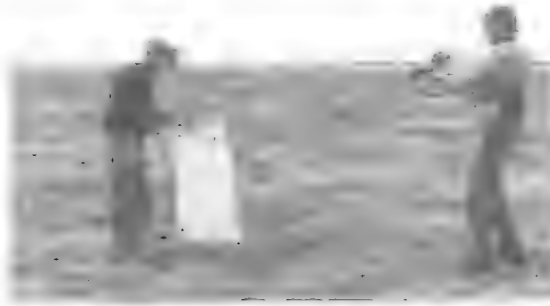


FIG. 1. Charles Tanner (left) capturing a specimen of *O. microlepidotus* on the Moneypine near Windorah, SWQ. This sequence was filmed by Vic Martin, 1974. (Photo JAC)





FIG. 2. The first 'milking' of a specimen of *O. microlepidotus*, by Charles Tanner, 1974. (Photo JAC).

National Museum of Victoria. Many years later, following receipt of a preserved head/tail of this species at the Queensland Museum, he and one of us (JAC) relocated this long-lost species in south western Queensland. Charles Tanner caught his and the world's first live specimen in Spring, 1974, near Windorah, SWQ (Fig. 1.). In one week he collected 13 large, healthy specimens which formed the nucleus of a collection on which an extensive research programme was based. From study of those specimens and their progeny, a series of papers was published on *O. microlepidotus*. Over some 20 years, the least well-known elapid species in Australia became probably its best known (Covacevich & Wombey, 1976; Sutherland et al., 1978; Covacevich et al., 1981; Shine & Covacevich, 1983; Covacevich & Tanner, 1983; Broad et al., 1979b; Morrison et al., 1984; Covacevich, 1987; Covacevich, 1990; Covacevich, 1994).

In the Australian Venom Research Unit, Department of Pharmacology, the University of Melbourne, a study to examine the antibodies to snake venom components and antivenoms in the sera of herpetologists is underway. Charles Tanner had a particular interest in this project. He had not only two types of antibodies to eight different venom proteins, but also antibodies to the principle protein in antivenom. Thus, as his and the other sera continue to be explored, his contributions to medical research will continue! (Fig. 2.).

Two species have been named to recognise his many contributions to herpetology: *Pseudonaja affinis tanneri* (Worrell, 1961), *Lygisaurus tanneri* Ingram & Covacevich, 1988.

In addition to his contributions to toxinology and herpetological taxonomy, Charles Tanner will be remembered for his wisdom and for the generous way he shared his knowledge with both amateur and professional herpetologists. He will also be remembered for his dry sense of humour. Nothing encapsulates his wit and humour so well as a conversation he had with one of us (JAC) in 1993. It went: JAC: 'Charles, how are you? CT: Fine thanks, except that my memory, especially my short-term memory, is shot to pieces. JAC: Hell, I'm sorry. That must be difficult for you. CT: It would be, if I could remember anything to worry about'. The words on a memorial erected on his former farm near Cooktown summarize: 'Passionate about the natural world (especially reptiles!), he contributed significantly in the fields of taxonomy and toxinology, and to knowledge of the natural history of turtles, crocodiles and elapid snakes. Adventurous, generous of spirit, witty, intelligent, and ruggedly individualistic, he was admired and respected by many. Remembered well by his friends and colleagues.

*Alis volat propriis*  
(He flies on his own wings).'

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